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Bulletin of the
British Museum (Natural History)

Studies in the genus *Hypericum* L. (Guttiferae)
7. Section 29. *Brathys* (part 1)

Norman K. B. Robson

Botany series Vol 16 No 1 29 January 1987

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Studies in the genus *Hypericum* L. (Guttiferae)
7. Section 29. *Brathys* (part 1)

Norman K. B. Robson

Department of Botany, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

A systematic account is given of the 61 shrubby species of *Hypericum* sect. 29 *Brathys*, which occur from Belize and the Greater Antilles to Peru and Bolivia. A discussion of the morphology, chromosome number (only one known), distribution, and evolution of the members of the section is included.

Sect. 30 *Spachium* sensu Robson (1977) is shown to comprise three distinct groups: (i) sect. *Spachium* sensu stricto (Central America, Greater Antilles, eastern U.S.A.), which is included in sect. 29. *Brathys*; (ii) sect. **Knifa** (Adanson) N. Robson, **stat. nov.** (S. American Cordillera, Central and North America, Cuba, tropical and southern Africa, east and south-east Asia, Australia); (iii) sect. **Trigynobrathys** (Y. Kimura) N. Robson, **comb. nov.** (S. America south of Amazonia and along the Cordillera, Australasia, south-east Asia).

The following other new taxa (**sp. nov.** or **subsp. nov.**) are described: *H. phellos* subsp. *oroqueanum* N. Robson (Colombia: Norte de Santandér/César), *H. acostanum* Steyerm. ex N. Robson (Ecuador: Loja, Morona-Santiago), *H. irazuense* Kuntze ex N. Robson (Costa Rica), *H. simonsii* N. Robson (Colombia: Magdalena), *H. papillosum* N. Robson (Colombia: Boyacá), *H. martense* N. Robson (Colombia: Magdalena), *H. maguirei* N. Robson (Ecuador: Azuay, Loja, El Oro), *H. gleasonii* N. Robson (Colombia: Norte de Santandér), *H. prietoi* N. Robson (Ecuador: Azuay), *H. cassiopiforme* N. Robson (Peru: Amazonas), *H. magdalenicum* N. Robson (Colombia: Magdalena; Venezuela: Zulia, Mérida), *H. valleanum* N. Robson (Colombia: Valle de Cauca), *H. sprucei* N. Robson (Ecuador: widespread; Peru: Piura), *H. recurvum* N. Robson (Peru: Amazonas, Junin, Pasco), *H. wurdackii* N. Robson (Peru: Amazonas), *H. costaricense* N. Robson (Costa Rica; Panama; Colombia: Bolivar, Antioquía), *H. bolivaricum* N. Robson (Colombia: Bolivar), *H. parallelum* N. Robson (Colombia: Norte de Santandér/

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Césâr), *H. marahuacanum* N. Robson (three subspecies): subsp. *marahuacanum* (Venezuela: Amazonas), subsp. *strictissimum* N. Robson (Colombia: Boyacá; Venezuela: Mérida), subsp. *chimantaicum* N. Robson (Venezuela: Bolivar), *H. horizontale* N. Robson (Colombia: Norte de Santandér, Santandér), *H. jaramilloi* N. Robson (Costa Rica; Colombia: Magdalena, Césâr/Norte de Santandér), *H. llanganaticum* N. Robson (Ecuador: Tungurahua, Napo), *H. selaginella* N. Robson (Colombia: Boyacá, Arauca, Cundinamarca), *H. cymobrathys* N. Robson (Colombia: Boyacá).

The following changes of rank (**stat. nov.**) are also made: *H. phellos* subsp. *platyphyllum* (Gleason) N. Robson, *H. loxense* subsp. *aequatoriale* (R. Keller) N. Robson, *H. caracasanum* subsp. *turumiquirense* (Steyerm.) N. Robson. Two others are also new combinations (**comb. et stat. nov.**): *H. strictum* subsp. *compactum* (Triana & Planchon) N. Robson, *H. lancioides* subsp. *congestiflorum* (Triana & Planchon) N. Robson.

1. Introduction

It has proved to be impracticable to complete the systematic part of this monograph of *Hypericum* L. in the order in which the sections were treated in part 1 (Robson, 1977). This account of sect. 29. *Brathys*, which is part 7 of an estimated nine parts*, has been completed next after part 3 (sects 1–6a) as a result of work on it for *Flora Neotropica*. The distributional area of the shrubby members of sect. *Brathys* (Belize and the Greater Antilles to Bolivia) falls wholly within the area of that Flora.

The publication of part 7 out of order has necessitated the abandoning of the double enumeration started in part 3, where each species has a running generic number as well as a sectional one. In parts 4–8, therefore, the species will have only sectional numbers; but a continuous enumeration will be included in part 9, along with addenda, corrigenda, and a revised sectional key.

The division of sect. *Brathys* sensu lato into two sections, 29 *Brathys* (trees, shrubs, and shrublets, centred north of Amazonia) and 30 *Spachium* (subshrubs and herbs, centred south of Amazonia) has proved to be incorrect. Sect. *Brathys* in fact includes a group of subshrubs and wiry herbs that contains the type of sect. *Spachium* (*H. gentianoides* (L.) Britton, Sterns & Poggenb.), thus extending the area of the section northward to eastern U.S.A. In addition, the herbaceous *H. piriai* Arechav. (including *H. hilaireanum* L.B.Sm. ≡ *H. tenuifolium* St. Hil. non Pursh) represents a development from Sect. *Brathys* in which the flower has apparently become adapted for specialized insect pollination in a manner partially analogous to those of sects *Elodes* and *Adenotrias*. It has been treated as an extension of variation of Sect. *Brathys*, and its inclusion extends the area of this section south of Amazonia to south-eastern Brazil and Uruguay (Fig. 1).

The remainder of sect. *Brathys* sensu lato divides into two sections. One of these is centred (i.e. has the species with the most primitive characters) in the Andes of Venezuela and adjacent Colombia, extending southwards along the Cordillera to Chile and northwards to Canada; and it also occurs in SE Asia and Australasia (*H. japonicum* Thunb. ex Murray) and Africa and Madagascar (*H. lalandii* group). Until now this section, which includes both shrubs and herbs, has not been recognized as distinct and therefore has no name. It does, however, include the type species of the genera *Knifa* Adanson (*H. mutilum* L.) and *Tridia* Korthals (*H. japonicum* Thunb. ex Murray), both of which were treated as series of *Sarothra* sect. *Spachium* by Kimura (1951). I have therefore chosen *Knifa* as the epithet for this new section:

Hypericum section **Knifa** (Adanson) N. Robson, **stat. nov.**

Knifa Adanson, *Fam. Pl.* **2**: 44, 541 (1763).

Tridia Korth. in Tijdschr. Natürl. Gesch. Physiol. **3**: 17(1836).

Sarothra sect. *Spachium* series *Knifa* (Adanson) Y. Kimura in Nakai & Honda, *Nova Fl. Japonica* **10**: 233 (1951) 'Kniffa'.

Sarothra sect. *Spachium* series *Japonica* Y. Kimura, *tom. cit.*: 233 (1951).

Type: *H. mutilum* L. (Y. Kimura, 1951, lectotype).

The other section, comprising shrubs, suffrutices, and herbs, is centred in south-eastern Brazil and extends in area to Uruguay, northern Argentina, and Peru and thence northward along the

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* For part 1 see Robson (1977); for part 2 see Robson (1981); for part 3 see Robson (1985).

Cordillera to Venezuela. It also occurs in Australasia and SE Asia (*H. gramineum* Forster f.). The type of Kimura's *Sarothra* sect. *Trigynobrathys* (*H. myrianthum* Cham. & Schlecht.) belongs to this section (although that epithet is not especially appropriate to the concept adopted here), as well as the type of sect. *Brathys* subsect. *Connatum* R. Keller (*H. connatum* Lam.):

Hypericum section **Trigynobrathys** (Y. Kimura) N. Robson, **comb. nov.**
Sarothra section *Trigynobrathys* Y. Kimura in Nakai & Honda, *Nova Fl. Japonica* **10**: 233 (1951).
Type: *H. myrianthum* Cham. & Schlecht. (*Sarothra myriantha* (Cham. & Schlecht.) Y. Kimura).

The characters by which species in these three sections may be recognized can be summarized as follows:

1. Leaf lamina with short, sometimes thick basal insertion, pairs free or united by interfoliar ridge or very rarely more broadly united; inflorescence-branching usually pseudo-dichotomous or monochasial .... sect. 29. *Brathys*
   Leaf lamina with long narrow basal insertion, pairs free or united by interfoliar ridge or by lamina proper, sometimes with bases decurrent or leaves perfoliate; inflorescence-branching pseudo-dichotomous or monochasial or dichasial 2
2. Leaves narrowed at the base or wholly narrow, united by interfoliar ridge, with basal vein single, venation pinnate or 1-nerved, or, if (secondarily) amplexicaul and 3–5-nerved (*H. majus* and *H. lalandii* groups p.p.), then midrib branches absent of weak .... sect. 30. *Knifa*
   Leaves amplexicaul with 3–7 basal veins and midrib clearly branched, the leaf pairs usually decurrent or sometimes perfoliate .... sect. 31. *Trigynobrathys*

Morphology (Fig. 2)

The species in sect. 29 *Brathys* vary from small trees (up to 4 m in height) to prostrate shrublets or wiry herbs. They all lack dark glands completely and have no resin glands on the lower surface of the leaf (the latter are common in sect. 3 *Ascyreia* but not in sect. 1 *Campylosporus*), and there are no fringing glands on leaves, sepals, and petals. It appears that all have marginal punctiform leaf glands (although these are often very small), and the laminar glands in the leaves are also always punctiform. In the sepals and petals, however, the laminar glands vary from wholly linear to wholly punctiform.

(a) *Leaves*

The reduction of the laminar leaf glands from lines to dots is not here associated with the development of reticulate venation, as it is in sect. 1 *Campylosporus* (Robson, 1981: 80, Fig. 11). In the species of sect. *Brathys* with the most primitive characters (1 *H. terrae-firmae*) the venation is parallel and open, even though the laminar glands are punctiform. The primary venation remains open in nearly all the woody species, thus allowing reduction to 1-nerved leaves to occur in several parts of the section. Only in some of the relatively primitive species, e.g. 24 *H. magniflorum*, is there a clear tertiary reticulum.

In sect. *Brathys* the ultimate fate of the leaves has proved to be of major taxonomic importance. In the most primitive state (found in 1 *H. terrae-firmae* and 2 *H. styphelioides*) the leaves are free and completely deciduous, leaving a rhombic leaf scar. In all other species they are wholly or partly persistent, the persistent part being eventually shed with the cortex of the stem internode; and the leaf bases are usually united by an interfoliar ridge. The ultimate fate of these leaves depends on their thickness and size. Where they are thick and long, they break off without fading, leaving a perceptible part of the base (25 *H. gleasonii* to 61 *H. cymobrathys* except 54 *H. millefolium*). Where they are thin and long, they tend to droop and wither on the stem (3a *H. phellos* subsp. *phellos* in part, 10 *H. simonsii*, 11 *H. papillosum*, and 24 *H. magniflorum*). Where these thin leaves have (in evolution) become smaller or narrower and thicker, they either fall at the apparent base (3 *H. phellos* and 4 *H. garciae*) or persist and wither (Spp. 5–9, 12–23), tending to become secondarily appressed if the base is narrow (e.g. 8 *H. stenopetalum*) and depressed if it is broad (e.g. 16 *H. cuatrecasii*). Finally, in 54 *H. millefolium*

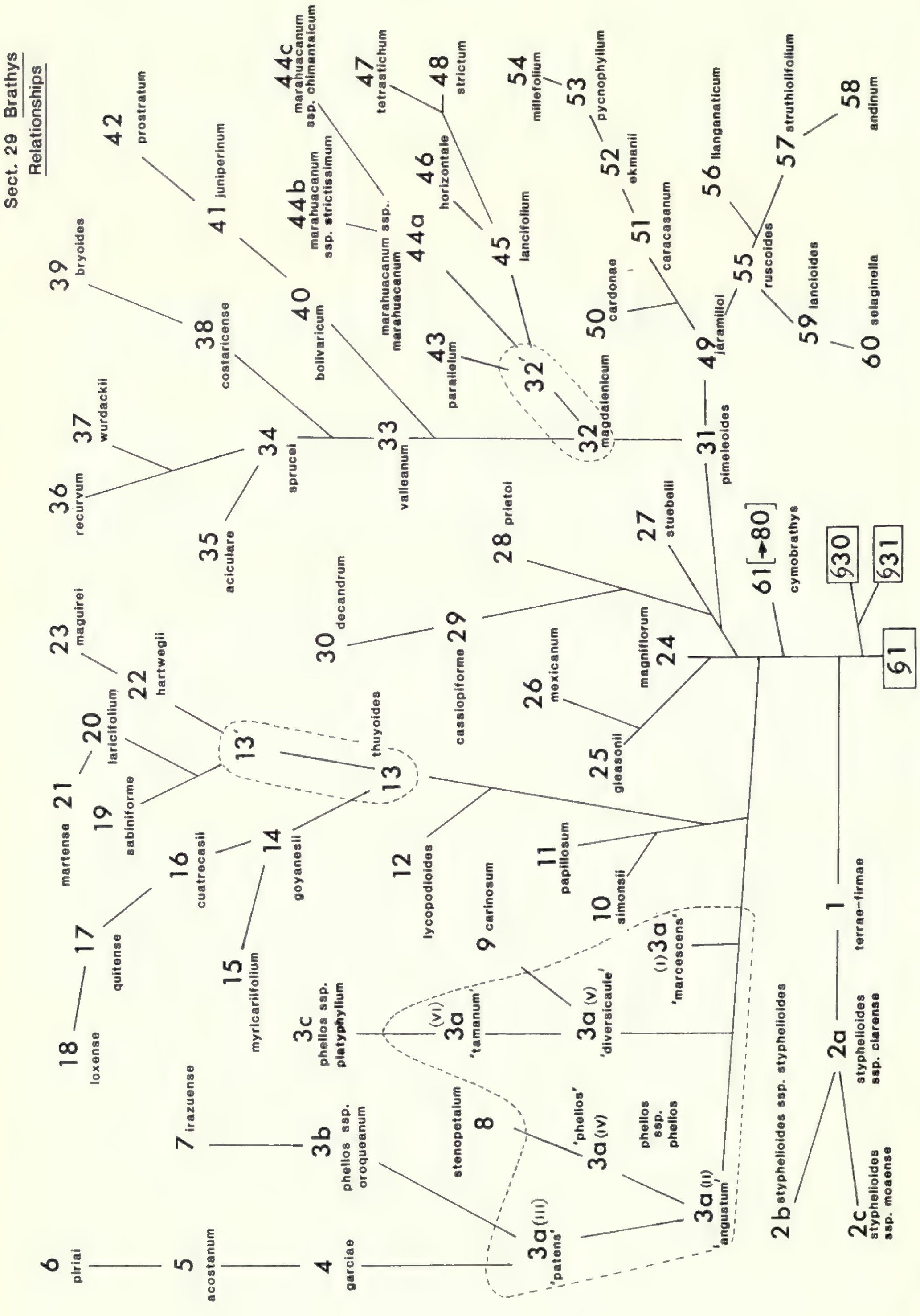
Sect. 29 Brathys
Relationships
6 piriai
5 acostanum
4 garciae
3a(iii) 'patens'
3b phellos ssp. oroqueanum
7 irazuense
18 loxense
17 quitense
16 cuatrecasii
15 myricariifolium
14 goyanesii
13 thuyoides
13'
19 sabiniforme
20 laricifolium
21 martense
22 hartwegii
23 maguirei
12 lycopodioides
11 papillosum
10 simonsii
9 carinosum
8 stenopetalum
3c phellos ssp. platyphyllum
3a(vi) 'tamanum'
3a(v) 'diversicaule'
(i)3a 'marcescens'
3a(iv) 'phellos'
phellos ssp. phellos
3a(ii) 'angustum'
2b styphelioides ssp. styphelioides
2a styphelioides ssp. clarense
2c styphelioides ssp. moaense
1 terrae-firmae
25 gleasonii
26 mexicanum
24 magniflorum
29 cassiopiforme
30 decandrum
28 prietoi
27 stuebelii
61[→80] cymobrathys
§30
§31
§61
35 aciculare
36 recurvum
37 wurdackii
34 sprucei
33 valleanum
38 costaricense
39 bryoides
40 bolivaricum
41 juniperinum
42 prostratum
43 parallelum
32 magdalenicum
32'
44a marahuacanum ssp. marahuacanum
44b marahuacanum ssp. strictissimum
44c marahuacanum ssp. chimantaicum
marahuacanum ssp.
45 lancifolium
46 horizontale
47 tetrastichum
48 strictum
54 millefolium
53 pycnophyllum
52 ekmanii
51 caracasanum
50 cardonae
49 jaramilloi
31 pimeleoides
55 ruscoides
56 llanganaticum
57 struthiolifolium
58 andinum
59 lancioides
60 selaginella

Fig. 1 Sect. 29 *Brathys*: Relationships of the 80 species and related sections. For details of Spp. 62–80, see Part 8. Limits of taxa showing variation relevant to the diagram are indicated by an interrupted line.

the leaves are very small and remain attached to the stem, falling with it either when it disarticulates at the nodes or with the cortex.

In those taxa in which the leaves fall at the apparent base, the true base has become united with the stem, surviving only as a protuberance (e.g. in 4 *H. garciae*). Such leaves can be distinguished from the wholly deciduous leaves of *H. terrae-firmae* and *H. styphelioides* by the absence of a true leaf scar.

The order of these leaf characters in evolution would appear to have been: wholly deciduous – wholly persistent – partly deciduous – wholly persistent again (Spp. 5–9 and 62–80), see Fig. 2.

The leaf base mostly remains parallel-sided or only slightly narrowed before widening to form the interfoliar ridge; but in one group (31 *H. pimeleoides* in part and Spp. 49–53, 55, 59 in part) it narrows perceptibly to form a pseudopetiole. Where the lamina has narrowed to the width of the pseudopetiole, however, members of this group cease to appear petiolate and have to be described as (secondarily) sessile (Spp. 54, 56–59 in part).

(b) *Inflorescences*

The inflorescence in woody members of sect. *Brathys* is nearly always 1-flowered (the primitive state in the genus). Only in a few of the more primitive species (e.g. 3 *H. phellos*, 26 *H. mexicanum*, and 61 *H. cymobrathys*) is there any development of cymose branching; and even then it is not usually constant and never elaborate. Apart from this relatively weak tendency to produce monochasia, the inflorescence in woody species is always strictly a synflorescence with variation resulting from different types and aggregations of 1-flowered branches. The basic form is the pseudo-dichotomy, i.e. the development of equal foliate branches from the axils of the leaf pair immediately below the flower. This is the only type of acropetal inflorescence development in the section; but the upper lateral branches are also often floriferous, and the relative frequency of these two modes of branching can be of taxonomic value. Thus in 10 *H. simonsii*, for example, the flowers are solely on lateral branches, whereas in 21 *H. martense* the majority of the pulviniform plant consists of a pseudo-dichotomous synflorescence, with the branches of the latest pseudo-dichotomies bearing lateral flowering branches (Fig. 8).

The development of a suffruticose or herbaceous habit (6 *H. piriai* and Spp. 62–80) is accompanied by the elaboration of monochasial cymose inflorescences.

(c) *Flowers and fruits*

In section *Brathys* the perianth is normally pentamerous, with the sepals appressed to the petals. These are longer than the sepals and usually spreading ('flowers stellate'), but in small flowers they may remain ascending ('flowers obconic'). The sepals vary in width and hence in the number of nerves, which may be of taxonomic significance, as may also be the aspect (plane to incurved-cucullate). Variation in petal shape and size may help to separate related species; but the degree of development of the apiculus, though striking, is not discontinuous enough to be of taxonomic value.

The number and size of the stamens are correlated in general with flower size as a whole, but the woody species with the fewest stamens (35 *H. decandrum*, which can have as few as 5) does not have the smallest flowers. That distinction belongs to 42 *H. prostratum*, in which they can be as small as 4 mm in diameter. Among the herbs *H. gentianoides* can have as few as 5 stamens and also has the smallest flowers.

The styles vary in number from 5 (*H. terrae-firmae, H. styphelioides*) to 3, 4 as usual being an apparently unstable number, not characteristic of any one species. The majority of species have 3 styles, but in three advanced woody species this trend has been reversed so that an increased number (4–5) of styles is associated with very small flowers (41 *H. juniperinum* = *H. brathys*), 42 *H. prostratum*, and 60 *H. selaginella*). The form of the styles (outcurving, incurving, etc.) may be taxonomically useful. The stigma is primitively narrow but has frequently become broader, usually in a capitate form; in one group (Spp. 51–53) the style apex is clavate. The ovary and capsule remain enclosed in the perianth except when the flower is open, and so it is not always easy to observe them in herbarium specimens. Nevertheless, their shape varies and can be utilized taxonomically.

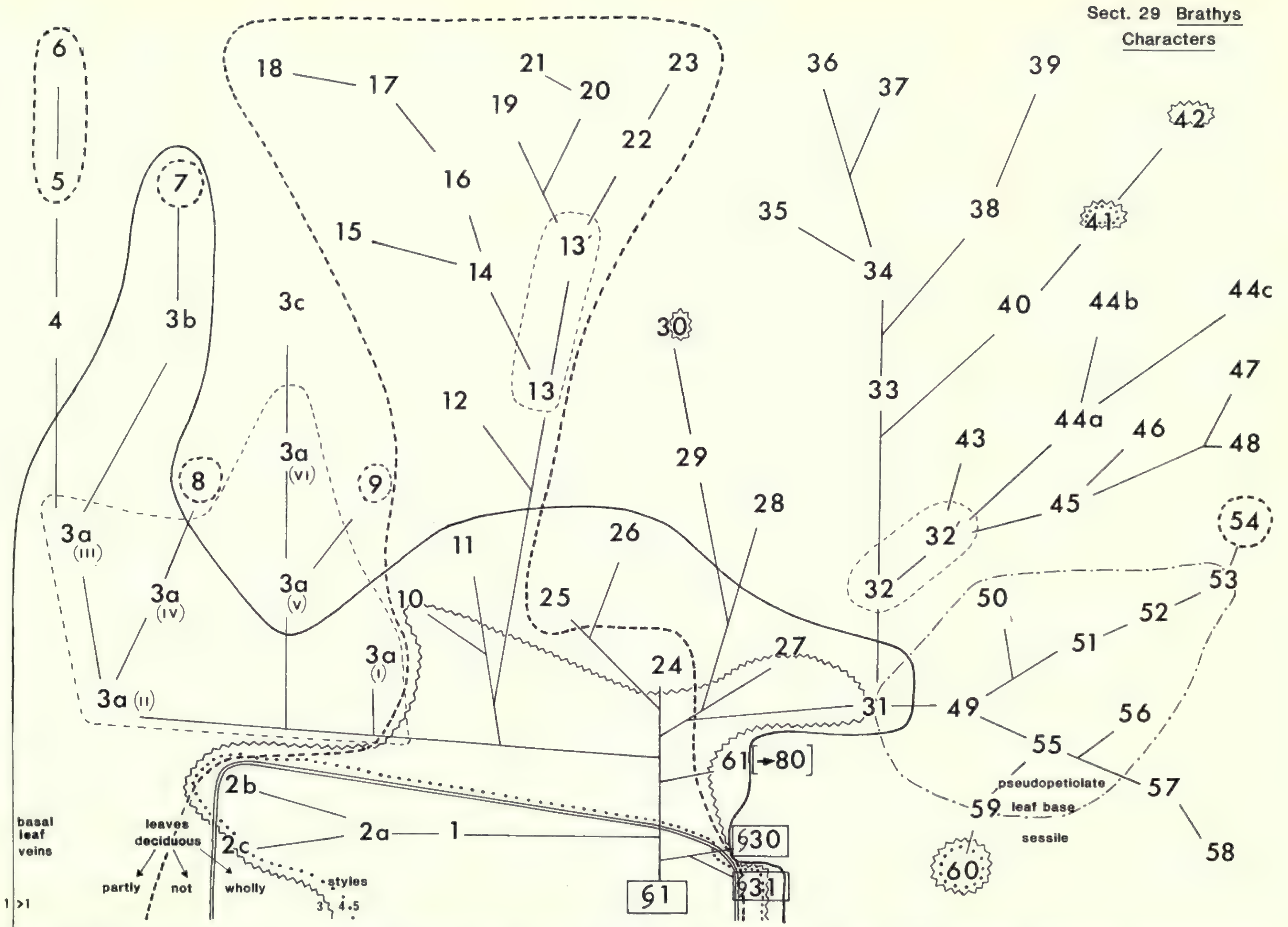
Sect. 29 Brathys
Characters
6
5
4
7
3b
3c
18
17
16
15
14
21
20
19
23
22
13
13
12
30
29
28
26
27
25
24
11
10
3a (III)
3a (IV)
3a (II)
3a (VI)
3a (V)
3a (I)
8
9
36
37
35
34
33
32
32
31
39
38
42
41
40
44b
44c
44a
43
47
46
48
45
54
53
52
51
50
49
56
55
57
58
pseudopetiolate
leaf base
59
sessile
60
61 [→80]
630
931
61
1
2a
2b
2c
basal
leaf
veins
1 >1
leaves
deciduous
partly
not
wholly
styles
3
4-5

Fig. 2 Sect. 29 *Brathys*: Limits of certain characters within the section and related sections. Note the isolated apomorphic occurrences of 4–5-styled species. Limits of taxa showing variation relevant to the diagram are indicated by a narrow interrupted line.

Cytology and hybrids

Very little cytological work has been done on the major part of Sect. *Brathys*, the only recorded chromosome count for a woody species being n = 12 for 7 *H. irazuense* (Part 2: table 7). As this is the primitive number for the whole genus (Part 2: 150), there is no available information about possible chromosome variation within the woody members of the section. The numbers n = 6, 12, 24 have been recorded for herbaceous species (see part 8).

Hybrids in sect. *Brathys* are apparently very rare. The only specimen seen that might be a hybrid was collected in Costa Rica (*J. & C. Taylor* 11757 (NY)) and looks like *H. irazuense* × *costaricense*.

Distribution and evolution (Fig. 3)

In parts 2 and 3 it was shown that sect. 29 *Brathys* is directly related to the basic, African sect. 1 *Campylosporus,* the taxon in it that is most closely related to *H. terrae-firmae* being *H. revolutum* subsp. *keniense* from the East African mountains (Figs 1–3). Sect. 30 *Spachium*, as has been shown above, must be divided into three parts, the name-giving part being included in sect. 29 *Brathys*. The other two parts, sects 30 *Knifa* and 31 *Trigynobrathys*, are more closely related to each other than either is to sect. *Brathys*. All three sections, 29–31, would seem to have stemmed from an early westward development from the original *Hypericum* stock in the eastern part of west Gondwanaland, i.e. in what was to become Africa. This western group appears to have divided into a northern (sect. *Brathys*) and a southern subgroup, the latter also having divided into a northern group (sect. *Knifa*) and a southern group (sect. *Trigynobrathys*) as a result of (climatic?) changes in the Amazon region. It clearly migrated into what is now South America while contact between Africa and eastern South America was still possible, i.e. until the Lower Cretaceous (Turonian–100m yrs BP) (Raven & Axelrod, 1974; Owen, 1976; Howarth, 1981); but whether it had split into two before or after reaching that region is uncertain. From the evolutionary divergence pattern of *Hypericum* as a whole (Robson, 1981: Fig. 73; Robson, 1985; Fig. 1), it seems likely that the first split occurred in Africa.

For a temperate genus such as *Hypericum* that is confined in tropical latitudes to high altitudes, the ranges of the Cordillera act as highways of dispersion to which the species are restricted and along which they migrate and differentiate. It is therefore often possible to trace presumed evolutionary lines (clades or, more accurately, morphoclines) in sequence along one or more of the Andean ranges. If the variation is continuous, as it is for examples in 20 *H. laricifolium*, no infraspecific taxa can be recognized, even though the forms at the extreme ends of the range of this species ('*H. laricoides*' in Venezuela and '*H. acerosum*' in Peru) look very different from the primitive form from northern Ecuador.

If the variation becomes discontinuous, on the other hand, one finds a geographical replacement series of taxa each more advanced (apomorphic) than the one before. In such a clade it is frequently difficult or impossible to discover any apomorphic character in the less advanced taxon that would enable one to conclude that it had continued to evolve independently subsequent to its isolation from the more advanced one. In such clades, therefore, where it is difficult to believe in the Hennigian maxim that one taxon is automatically altered when it gives rise to another (i.e. that at each speciation the cladogram must dichotomize), I have depicted the relationship (Figs 1–3) by a line, not a dichotomy.

(a) *Wide disjunctions*

The majority of the primitive species in sect. *Brathys* occur in, or are confined to the mountains near, the Colombian-Venezuelan border area or to adjacent areas in Boyacá (Colombia) and Mérida, Táchira or Trujillo (Venezuela); but the most primitive (plesiomorphic) characters are found in the species from Belize (1 *H. terrae-firmae*) and Cuba (2 *H. styphelioides*), species that are so closely related that they have sometimes been united under the latter name, e.g. by Standley & Williams (1961). The question therefore arises as to whether (i) the original members of sect. *Brathys* migrated and differentiated southward from Belize/Cuba to Colombia/Venezuela before isolation of the two groups, or (ii) the differentiation took place

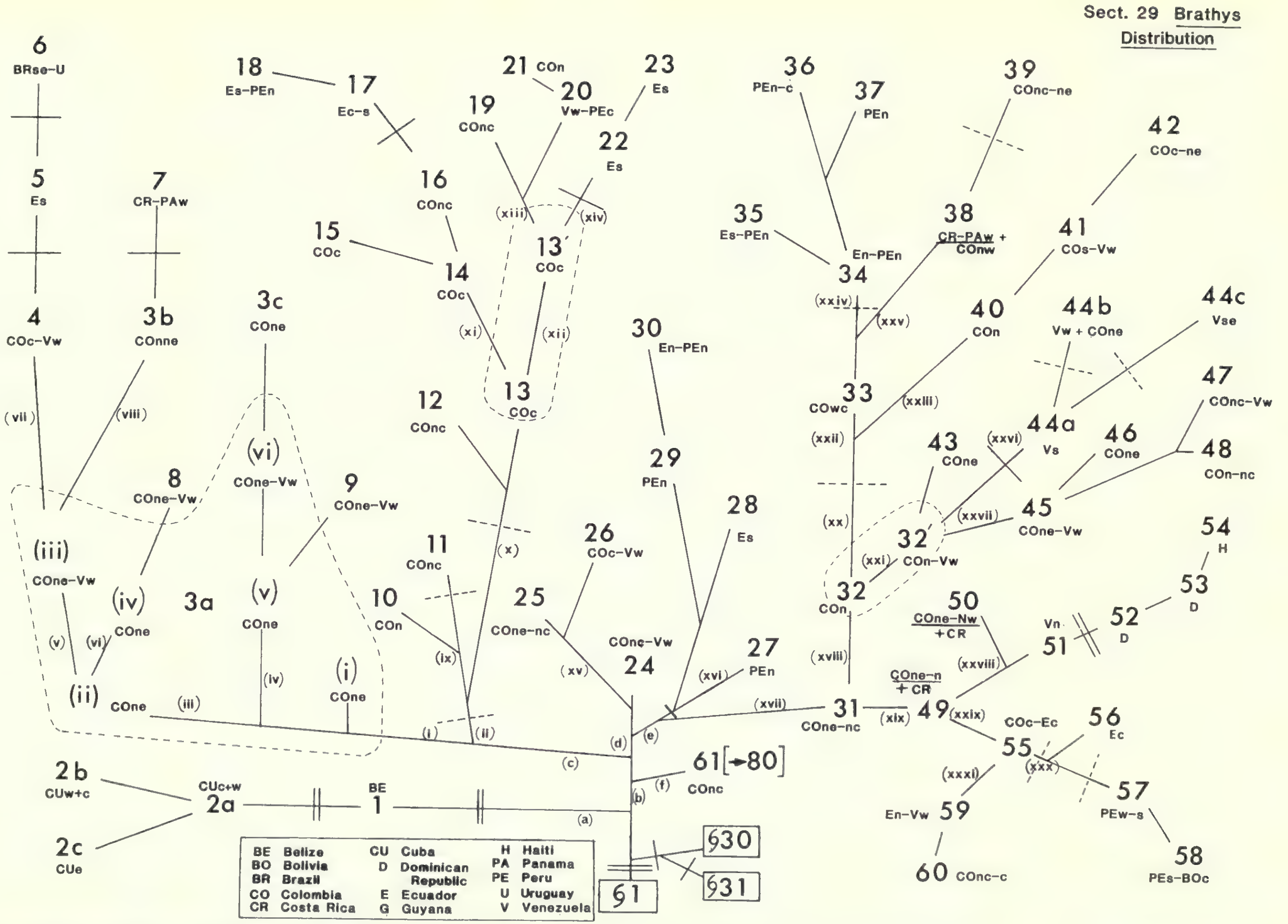
Sect. 29 Brathys
Distribution
6 BRse-U
5 Es
4 COc-Vw
7 CR-PAw
3b COnne
3c COne
3a
18 Es-PEn
17 Ec-s
16 COnc
15 COc
14 COc
19 COnc
21 COn
20 Vw-PEc
23 Es
22 Es
13′ COc
13 COc
12 COnc
11 COnc
10 COn
30 En-PEn
29 PEn
28 Es
27 PEn
26 COc-Vw
25 COne-nc
24 COnc-Vw
36 PEn-c
37 PEn
35 Es-PEn
34 En-PEn
33 COwc
39 COnc-ne
38 CR-PAw + COmw
42 COc-ne
41 COs-Vw
40 COn
44b Vw + COne
44c Vse
44a Vs
47 COnc-Vw
48 COn-nc
46 COne
43 COne
45 COne-Vw
32′ COn-Vw
32 COn
31 COne-nc
54 H
53 D
52 D
51 Vn
50 COne-Nw +CR
49 COne-n + CR
55 COc-Ec
56 Ec
57 PEw-s
58 PEs-BOc
59 En-Vw
60 COnc-c
2b CUw+c
2a CUc+w
2c CUe
1 BE
61[→80] COnc
§30
§31
61
(iii) COne-Vw
(ii) COne
(iv) COne
(v) COne
(vi) COne-Vw
(i) COne
8 COne-Vw
9 COne-Vw
(vii) (viii) (v) (vi) (iii) (iv) (i) (ii) (ix) (x) (xi) (xii) (xiii) (xiv) (xv) (xvi) (xvii) (xviii) (xix) (xx) (xxi) (xxii) (xxiii) (xxiv) (xxv) (xxvi) (xxvii) (xxviii) (xxix) (xxx) (xxxi)
(a) (b) (c) (d) (e) (f)
BE Belize
BO Bolivia
BR Brazil
CO Colombia
CR Costa Rica
CU Cuba
D Dominican Republic
E Ecuador
G Guyana
H Haiti
PA Panama
PE Peru
U Uruguay
V Venezuela

Fig. 3 Sect. 29 *Brathys*: Distribution of the 61 woody species showing major and minor disjunctions (══ across sea, ‒ ‒ across land (major), - - - - across land (minor)). Lower-case letters indicate north, east, west, south and central. Small roman figures indicate clades discussed in the text. Limits of taxa showing variation relevant to the diagram are indicated by an interrupted line.

northwards from South America to the Greater Antilles before isolation, or (iii) a uniform population was split and the two groups evolved in isolation (Fig. 3a/b). What *is* clear is that this distribution gives strong support to the theory that the first land link between South America and North American was by way of the Greater Antilles (Rosen, 1976, 1985; Robson, 1981: 213; Melville, 1981: 247).

The remaining evolution of the section has been wholly within South America, except for: (i) four species that have reached Costa Rica/Panama after the establishment of the second land link (Isthmus of Panama), (7 *H. irazuense*, 38 *H. costaricense*, 49 *H. jaramilloi*, and 50 *H. cardonae*), (ii) three shrubby species in Hispaniola (52 *H. ekmanii*, 53 *H. pycnophyllum*, and 54 *H. millefolium*), and (iii) the derivatives of 61 *H. cymobrathys*, which occur throughout Central America and the Greater Antilles and extend their area of distribution into eastern U.S.A. The three Hispaniolan shrubs terminate a clade that originates with two of the Costa Rican species, which also occur in the basic area of the Colombian-Venezuelan border (49 *H. jaramilloi*, 50 *H. cardonae*) (Fig. 3, clade xxviii). Occupying an intermediate position is 51 *H. caracasanum* of northern Venezuela, of which the more advanced subspecies (51b subsp. *turmiquirense*) is found at the north-eastern extreme of the Andean range and is also morphologically close to 52 *H. ekmanii*. These data suggest that the ancestor of the Hispaniolan species reached that island either directly by long-distance dispersal or via the Lesser Antilles, which, according to the above mentioned theory, would by then have arisen as a result of volcanic action; but overland access before the separation of the Greater Antilles from South America cannot be ruled out. A three-fold origin of Hispaniola from parts previously associated respectively with Yucatan, eastern Cuba, and the Bahamas, such as has been proposed by Rosen (1985), would make the overland route less likely (see also p. 91).

The immediate derivatives of 61 *H. cymobrathys* are three species of the Colombian and Venezuelan Andes (see Part 8). Of these the Colombian *H. chamaemyrtus* is the sister-species of the *H. gnidioides – H. gentianoides* group, which radiates from the Honduras Republic: south to Panama (*H. gnidioides*), north to north-eastern U.S.A. (*H. gentianoides*), and east to the Greater Antilles (*H. diosmoides* group). On the other hand, there is a wide geographical disjunction between the Venezuelan *H. pseudocaracasanum* and its sister-group in the south-eastern U.S.A. (*H. denticulatum* et aff.).

(b) *Species with leaves persistent or deciduous near the base* (Spp. 3–23)

In this group (Fig. 3 clade (c)) the leaves are rarely broadest above the middle, and so the leaf-venation is parallel to pinnate or 1-nerved, not flabellate. All species have leaves that are either wholly persistent or deciduous at the apparent base. They form two subgroups: clade (i) with leaves that are free (Spp. 3–9); clade (ii) with leaves that are united by an interfoliar ridge or rarely more intimately (Spp. 10–23).

Subgroup (i) radiates from 3 *H. phellos* of north-eastern Colombia and adjacent Venezuela. The variation in this species can be described; but it has not been possible to express this variation in a formal classification, apart from the recognition of two derivative subspecies. Subspecies *H. phellos* has therefore had to be differentiated plesiomorphically (i.e. by the possession of primitive characters), viz. by having plane or recurved (not incurved or revolute) leaves that are deciduous at the base of the free part (see p. 22).

Four separate derivative clades (iv, vi, vii, viii) end with taxa in which the leaves are secondarily wholly persistent, and in three of these (all but vii), the leaves are plane or incurved. The taxa in these three are all distributed in or near the Colombia-Venezuela border area near *H. phellos* except 7 *H. irazuense* (Costa Rica and adjacent Panama), which is confined to the nearest high ground in Central America to the Colombian Cordillera and is apparently derived from *H. phellos* subsp. *oroqueanum* (César/Norte de Santandér border).

In clade (vii) the tendency for the margin of coriaceous leaves to become reflexed (3a iii *H. phellos* subsp. *phellos* 'patens') is exaggerated, so that in 4 *H. garciae* it is revolute, hiding most of the lower lamina. In this species, which has a disjunct distribution in the central Colombia/western Venezuela area, the leaves tend to become narrow and sometimes longer, a tendency that is more evident in 5 *H. acostanum*, a local species of southern Ecuador that is smaller and less woody than *H. garciae*. Although isolated from the nearest *H. garciae* population by a wide disjunction (central Colombia to southern Ecuador), *H. acostanum* is separated from the species that terminates clade (vii) by an even wider one. 6 *H. piriai* is a woody herb of south-eastern Brazil and Uruguay in which the flowers have apparently become adapted to specialized insect-pollination. Thus the stamen fascicles have the filaments united for more than half way (as in, say, *H. elodes*), and two pairs of fascicles are more or less completely united. The petals are oblique to erect, sometimes making the flower pseudo-tubular, again as in *H. elodes*. How the gap between southern Ecuador and south-eastern Brazil was traversed is not clear; quite possibly it was by ancient long-distance dispersal. I have not yet discovered any similar disjunctions, but the morphocline southward along the Andes to Ecuador suggests that a vicariant interpretation is unlikely to be correct.

An early offshoot of clade (ii) comprises two isolated species (clade ix) in which the relatively large herbaceous leaves fade and droop while on the stem. 10 *H. simonsii* is confined to the northern part of the Sierra de Santa Marta (Magdalena), whilst 11 *H. papillosum* has a restricted distribution in Boyacá. In the remainder of the clade (ii) the leaves are smaller and either broad-based and deflexed (clade xi) or narrow-based and spreading only (clade xii). At the extremes of clade (xi) the leaves become too narrow to droop and so remain spreading (15 *H. myricariifolium*, 18 *H. loxense* in part). The species at the base of these clades (13 *H. thuyoides*) has a vicariad that is scarcely more than subspecifically distinct (12 *H. lycopodioides*), in which the leaves have become coriaceous. *H. thuyoides* itself, from central Colombia (Cundinamarca), is variable, with the broader-leaved (typical) form near clade (xi) and the narrower-leaved form ('genistoides') at the base of clade (xii). Clade (xii), in turn, divides into two distinct subclades: in one (xiv), the areas of 22 *H. hartwegii* and 23 *H. maguirei* represent a major disjunction to southern Ecuador, whereas in the other (xiii), *H. thuyoides* is near the origin of two trends initially in opposite directions, respectively northwards to Boyacá (19 *H. sabiniforme*) and southward to northern Ecuador (20 *H. laricifolium*). As has already been mentioned, *H. laricifolium* shows continuous variation southwards to central Peru and northwards to western Venezuela; but the morphologically reduced population further north, in the Sierra Nevada de Santa Marta (Magdalena) is sufficiently distinct to warrant specific recognition (21 *H. martense*).

(c) *Species with leaves with sheathing leaf-bases or marginal secretions* (Spp. 24–26, 61)

In contrast to the early offshoot (f) in Boyacá in which the oblong to elliptic leaves of the basic species have parallel venation (61 *H. cymobrathys*), nearly all early members of clade (d) (Fig. 3) have leaves broader above the middle with flabellate venation. A partial exception is 24 *H. magniflorum*, in which the Boyacá population has parallel-veined leaves, but the more northern one (straddling the Colombia-Venezuela border) has flabellate venation. *H. magniflorum* is also exceptional in that the leaves are relatively thin and droop when fading, instead of breaking off above the base like those of all the other species. It forms the base of one sub-branch of Branch (e) (clade xv), in which the broad, flabellate-veined leaves have sticky marginal leaf secretions, capitate stigmas, and usually a cymose inflorescence. 25 *H. gleasonii* occurs in the border area of Colombia/Venezuela, whereas 26 *H. mexicanum* has its primitive form in Boyacá and Cundinamarca and differentiated back northwards into the area of *H. gleasonii*.

(d) *Species with incurved-cucullate leaves but no marginal secretions* (Spp. 27–30)

Apart from those species with marcescent or secreting leaves in clade (xv) there remains clade (e), which splits into two subclades, (xvi) with leaves cucullate at the apex and (xvii) in which they have a plane apex (apart from a few of the more specialized species where the apex is somewhat cucullate).

The basic species of clade (xvi), 27 *H. stuebelii*, is a northern Peruvian relict, the area of which is thus separated from that of its nearest relatives in north-central Colombia by a considerable disjunction. All the other members of this group are confined to the south Ecuador/north Peru region except 30 *H. decandrum*, which has extended its area into north Ecuador. *H. stuebelii* has leaves broader than those of *H. magniflorum*, with flabellate venation; but the leaves of the other species (Spp. 28–30) are smaller and narrower with only a midrib or, at most, one pair of vein branches. Like *H. stuebelii*, 28 *H. prietoi* and 29 *H. cassiopiforme* appear to be relicts, but 30 *H. decandrum* is more widespread.

(e) *Species with sessile leaves deciduous above the base but not incurved-cucullate* (Spp. 31p.p.–48).
The primitive form of 31 *H. pimeleoides*, which is found in the Cerro de Oroque (César/Norte de Santandér), has large, broad, sessile, plane leaves; but within the range of this species are forms where the leaf base has narrowed to a pseudopetiole. The remaining major woody clades in sect. *Brathys* are respectively characterized by these two leaf forms, the species of clade (xviii) (Spp. 32–48) having sessile leaves, whereas in all but some extreme species of clade (xix) they are pseudopetiolate.

In clade (xviii) the basic species, 32 *H. magdalenicum*, is almost confined to the isolated northern Sierra de Santa Marta (Magdalena) and the adjacent Sierra de Perijá on the border with Venezuela. Apart from 43 *H. parallelum*, a close relative with smaller, densely imbricate leaves isolated on the Cerro de Oroque, this variable species has given rise to two clades, the members of which differ by a complex of characters. Clade (xx), which derives from the more primitive, broader-leaved form of the species, includes species with leaves that twist as they spread. This character is evident only where (a) the leaves are long enough to twist at all and (b) the internodes are not too short to preclude individual twisting. In two extreme species, 35 *H. aciculare* and 42 *H. prostratum*, the leaves are often too short to twist, while in 36 *H. recurvum* and 37 *H. wurdackii* the internodes are too short to allow it.

The two subsidiary clades of clade (xx) each has a relict basic species, both of which occur at a considerable distance to the south of the *H. magdalenicum* area. In clade (xxii), 33 *H. valleanum* (Colombia: Valle de Cauca) forms a stepping-stone to the species of clade (xxiv), which are all from Ecuador and Peru. Of these, 34 *H. sprucei* occurs from northern Ecuador to northern Peru, with the distribution of the derivative 35 *H. aciculare* overlapping its area in south Ecuador and just extending into Peru. The species with recurving leaves (36 *H. recurvum*, 37 *H. wurdackii*) are in north and central Peru, *H. wurdackii* being a bizarre relict with densely imbricate leaves forming four 'wings'.

Clade (xxv) proceeds along the Cordillera from *H. valleanum* in the opposite direction to that of clade (xxiv). A small population of 38 *H. costaricense* is found on the Bolivar/Antioquía border as well as the main one in Costa Rica and adjacent Panama, there being no suitably high ground between them. 39 *H. bryoides*, clearly a reduced version of *H. costaricense*, is confined to the South American Cordillera (Norte de Santandér to Boyacá).

In the relict basic species of clade (xxiii), 40 *H. bolivaricum* (Colombia: Bolivar), twisting leaves are combined with a condensed synflorescence and capitate stigmas, all characters that are found in the variable 41 *H. juniperinum* (= *H. brathys*). In the latter species, which is distributed from western Venezuela (Trujillo) to southern Colombia (Putumayo), there is a trend towards an increase in the number of styles and placentae from 3 to 4 and then to 5. The population from Cauca shows another trend, among 3–4-styled forms, from tall erect shrubs to smaller shrubs with decumbent stems. This trend is continued back north-eastward in 42 *H. prostratum*, a dwarf shrub or shrublet from the northern half of the Colombian Cordillera Oriental with stems decumbent to prostrate.

The remaining derivatives of 32 *H. magdalenicum* are all related to more advanced forms of that species (32′ in Fig. 3). Apart from 43 *H. parallelum* they form two clades: (xxvi) of which the members have polished, acicular leaves, rounded-incurved in section and twisting when large enough, and (xxvii) in which the species have leaves that are dull to metallic and flat to incurved but not usually rounded in section and become recurved not twisted. Clade (xxvi) comprises three geographically separate taxa that I have treated as subspecies of 44 *H. marahuacanum*. The subspecies with the largest flowers (44a subsp. *marahuacanum*) is confined to the Cerro Marahuaca in southern Venezuela (Amazonas), an isolated massif from which no other *Hypericum* species are known; and one of the derivative subspecies, 44c subsp. *chimantaicum*, is equally isolated further east, on the Chimantá Massif and Cima de Roraima (Bolivar) near the Guyana border. The remaining derivative subspecies, 44b subsp. *strictissimum*, occurs in two quite separate areas (Venezuela: Mérida and Colombia: Boyacá) and differs from subsp. *marahuacanum* in size and condensation of parts. In comparison with *H. marahuacanum*, the species of the *H. strictum* group (Spp. 45–48) are south-western in distribution, being confined to the area from Cundinamarca and Meta (Colombia) to western Venezuela. The relatively broad-leaved 45 *H. lancifolium*, from the Colombia-Venezuela border area, has a dwarf, high-altitude derivative, 46 *H. horizontale*. on the Colombian side of the frontier and a southern derivative complex (47 *H. tetrastichum*, 48 *H. strictum*) with *H. tetrastichum* extending from Boyacá northward into Venezuela and *H. strictum* occurring farther south.

(f) *Species with pseudopetiolate leaves deciduous above the base but not incurved-cucullate* (Spp. 31 p.p., 49–60)
The above heading is not strictly accurate in that a few of the advanced members of this group (clade xix) have developed a somewhat cucullate apex. But their leaves are linear and would not be confused with those of species in clade (xvi).

The species with pseudopetiolate leaves and their derivatives in clade (xix) (Spp. 49–60) would appear to have evolved relatively early in the history of sect. *Brathys*, as they have spread to almost the furthest limits of the shrubby part of the section (Hispaniola and Costa Rica to Bolivia). The basic species of this clade, 49 *H. jaramilloi*, has a disjunct distribution in northern Colombia (Cerro de Oroque, Sierra de Santa Marta) and Costa Rica; and an early species in the eastern subclade (xxviii), 50 *H. cardonae*, has a similar but wider distribution, in Costa Rica and the Colombia/Venezuela border region south to Boyacá. The rest of the species of this clade show a geographical replacement pattern eastward: 51 *H. caracasanum* in the mountains of northern Venezuela, with 51b subsp. *turumiquirense* at their extremity in Sucre, and the remainder (Spp. 52–54) in Hispaniola (see p. 9).

The second (westward) derivative clade of 49 *H. jaramillo*, clade (xxix), is based on 55 *H. ruscoides*, from south Colombia and north Ecuador, which gave rise southward to clade (xxx), a series of sessile-leaved species (56 *H. llanganaticum* in central Ecuador, 57 *H. struthiolifolium* in Peru, and 58 *H. andinum* in south Peru and Bolivia) with acute leaves and (at least initially) long styles with relatively narrow stigmas. In another direction, evolution resulted in two species with obtuse, cucullate leaves and short styles with relatively broad stigmas. Of these, 59 *H. lancioides* comprises a southern subspecies with a pseudo-dichotomous synflorescence (59a subsp. *lancioides*) and a northern one in which the flowering branches are lateral and congested (59b subsp. *congestiflorum*). A final southward development from the latter has resulted in the dwarf 60 *H. selaginella*, with prostrate or ascending stems and 3–5 styles and placentae.

2. Systematic treatment

Sect. 29. **BRATHYS** (Mutis ex L.F.) Choisy

Prodr. Monogr. Fam. Hypéric.: 38, 58 (1821).*

Small trees, shrubs, shrublets or wiry herbs up to 6 m tall, evergreen, glabrous or very rarely with simple hairs, without dark glands; branching below inflorescence lateral. *Stems* 4(6)-lined and ± compressed (ancipitous) when young, sooner or later becoming terete, eglandular; cortex exfoliating in strips or scales or irregularly; bark fissured, smooth. *Leaves* opposite, decussate, sessile to shortly petiolate, free or ± deeply united to form interfoliar ridge or very rarely bases of lamina proper united, base sometimes sheathing, deciduous at base or (more usually) above base or persistent and (in woody species) either fading or shed with cortex; lamina entire, with venation parallel or flabellate to pinnate or 1-veined, open or closed, with tertiary venation ± laxly reticulate; laminar glands punctiform; marginal gland dots dense, often very small; ventral resin glands absent. *Inflorescence* 1-flowered, with branching pseudo-dichotomous (usually from uppermost node) or 2–15-flowered and then with branching (within inflorescence) dichasial/monochasial from uppermost node, often with subsidiary branches from lower nodes; bracts and bracteoles foliar or reduced or sometimes transitional in form to sepals. *Flowers* stellate or occasionally obconic, homostylous. *Sepals* 5, free, persistent, erect in fruit, with margin entire; veins 3–11(–19); laminar glands linear to punctiform; marginal, submarginal and inframarginal glands absent. *Petals* 5, persistent, with apiculus subterminal to obsolete, acute to acuminate or obtuse; margin entire; marginal glands absent; laminar glands linear to punctiform. *Stamen fascicles* basically 5, very rarely distinguishable individually, usually forming a continuous narrow ring of 5–250 stamens (i.e. 1–50 per fascicle) or very rarely fascicles ± united 2 + 2 + 1, persistent; filaments very shortly united or very rarely united above midway; anthers yellow to orange, gland amber; pollen type VIII. *Ovary* with 3–5 parietal placentae, ∞-ovulate; styles 3–5, free with bases contiguous; stigmas small to broadly capitate or clavate. *Capsule* 3–5-valved, coriaceous to chartaceous, with valves obscurely narrowly longitudinally vittate, occasionally with 1–3 flattish vesicles. *Seeds* narrowly cylindric, shallowly carinate or not, without apical expansion; testa scalariform-reticulate to ribbed-scalariform.

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* Including *Sarothra* L. (1753), *Martia* sensu Sprengel (1826) pro parte, *Hypericum* sect. *Brathys* subsect. *Multistamineum* R. Keller (1893). *Hypericum* sect. *Brathys* subsect. *Spachium* R. Keller (1893), *Sanidophyllum* Small (1924), *Sarothra* sect. *Spachium* (R. Keller) Y. Kimura (1951), *Sarothra* sect. *Spachium* series *Eusarothra* Y. Kimura (1951), see Part 1 (Robson, 1977: 338); also *Hypericum* sect. *Sarothra* (L.) Reichardt in Martius, *Fl. Brasil.* **12**(1): 186 (1878).

BASIC CHROMOSOME NUMBER (x): 12; ploidy 1, 2, 4.

HABITAT: open grassland or among stones or sometimes in scrub or moist montane woodland, often along streams, in dry to locally wet areas of the Cordilleran páramo and subpáramo vegetation; 1600–4875 m. Also in open *Pinus* or *Pinus–Quercus* woodland or *Pinus* savannah or on sterile white sand (Spp. 1 and 2, in Belize and Cuba, 0–800 m); or in open *Pinus* forest or in cloud forest among limestone rocks (Spp. 52–54 in Hispaniola); 1300–3175 m. See part 8 for herbaceous species.

DISTRIBUTION: Belize, Cuba, Hispaniola; Costa Rica, Panama; Guyana (Roraima), Venezuela (Roraima, Chimantá, Marahuaca) and Andes of Venezuela, Colombia, Ecuador, Peru, and Bolivia: also (subshrubs and herbaceous species) Porto Rico, Honduras, Guatemala, Mexico, and south-eastern and eastern U.S.A.

80 species (+ 8 subspecies).

Key to sect. 29. *Brathys*

1	Leaves deciduous at base, leaving rhombic scar on stem; stem not articulate or with interfoliar ridges	2
	Leaves persistent (falling with cortex) or deciduous above base; stem articulate and/or with interfoliar ridges	5
2(1)	Leaves narrowly elliptic, acute, 16–30 mm long, chartaceous to subcoriaceous; sepals 14–22 mm long	1. ***terrae-firmae***(p. 18)
	Leaves narrowly obovate or, if oblong to elliptic, then acuminate or shorter (10–16 mm long) or thickly coriaceous; sepals 5–15 mm long (2. ***styphelioides***)	3
3(2)	Leaves narrowly elliptic to narrowly oblong, usually thinly coriaceous, spreading, often outcurving	2a. ***styphelioides*** subsp. ***clarense***(p. 21)
	Leaves oblanceolate to narrowly obovate, ± thickly coriaceous, ± densely imbricate, straight	4
4(3)	Leaves with 7–11 basal veins, glands not prominent	2b. ***styphelioides*** subsp. ***styphelioides***(p. 21)
	Leaves with 5–7 basal veins, glands prominent	2c. ***styphelioides*** subsp. ***moaense***(p. 22)
5(1)	Leaves persistent or deciduous immediately above base of free part; pseudo-dichotomous branches often absent or sparse	6
	Leaves deciduous above base, i.e. leaving base protruding from stem; pseudo-dichotomous branches often predominant	38
6(5)	Leaf bases either (i) sheathing or (ii) amplexicaul with stem fragile and articulated, the internodes and leaves falling as one	7
	Leaf bases free to perfoliate or shallowly cupped; internodes and leaves not as above	8

7(6) Leaf bases sheathing; leaves 10–18 mm long, withering; flowers 25–40 mm in diam. 24. ***magniflorum*** (p. 53)
Leaf bases amplexicaul; leaves up to 2 mm long, falling with internodes; flowers 5–7 mm in diam. .... 54. ***millefolium*** (p. 93)

8(6) Leaves free, the base sometimes indurated or fused with the stem 9
Leaves united by interfoliar ridge or lamina proper 22

9(8) Leaves becoming deflexed, marcescent; stem internodes without or almost without corky emergences .... 3a. ***phellos*** subsp. ***phellos*** (i) 'marcescens' (p. 25)
Leaves becoming deflexed to appressed but not marcescent; stem internodes with or without corky emergences 10

10(9) Leaves revolute, lower surface obscured, bases forming ± woody projections; stem internodes smooth 11
Leaves recurved to incurved, lower surface always visible; stem internodes usually with corky emergences 13

11(10) Leaves deciduous, 4–10 mm long, elliptic-oblong to linear; sepals ovate to lanceolate; shrub to 3 m tall .... 4. ***garciae*** (p. 26)
Leaves persistent, (8)10–40 mm long, linear; sepals narrowly lanceolate to linear or oblong; dwarf shrub to 0·8 m tall or suffrutex or herb 12

12(11) Flowers solitary, inflorescence-branching pseudo-dichotomous; flowers stellate; stamens not fasciculate; dwarf shrub .... 5. ***acostanum*** (p. 27)
Flowers 1–25, inflorescence-branching monochasial; flowers obconic to pseudotubular stamens 3(5)-fasciculate; suffrutex or perennial herb .... 6. ***piriai*** (p. 28)

13(10) Leaves with 3 basal veins, subcoriaceous 14
Leaves with 1 basal vein (venation wholly pinnate), chartaceous 19

14(13) Leaves recurved before falling .... 3a. ***phellos*** subsp. ***phellos*** (ii) 'angustum' (p. 25)
Leaves spreading to appressed before falling 15

15(14) Leaves deciduous 16
Leaves persistent 18

16(15) Leaves spreading, not or scarcely becoming appressed, elliptic to oblanceolate 3a. ***phellos*** subsp. ***phellos*** (iii) 'patens' (p. 25)
Leaves becoming or remaining appressed, oblanceolate to narrowly oblong 17

17(16) Leaves spreading, then appressed, before falling 3a. ***phellos*** subsp. ***phellos*** (iv) 'phellos' (p. 25)
Leaves remaining appressed, tetrastichous .... 3b. ***phellos*** subsp. ***oroqueanum*** (p. 25)

18(15) Leaves with 3 unbranched basal veins; flowers 25–30 mm in diam.; styles 9–10 mm long, 4–6 × as long as ovary .... 7. ***irazuense*** (p. 30)
Leaves with at least midrib branched; flowers 15–20 mm in diam.; styles 5–9 mm long, 2–4 × as long as ovary .... 8. ***stenopetalum*** (p. 31)

19(13) Leaves deciduous or subpersistent, midrib branched 20
Leaves persistent, 1-nerved .... 9. ***carinosum*** (p. 33)

20(19) Leaves with margins plane or recurved, spreading or becoming ascending, deciduous 21
Leaves with margin incurved, closely appressed, subpersistent 3c. ***phellos*** subsp. ***platyphyllum*** (p. 25)

21(20) Leaves broadly elliptic to obovate, not becoming ascending 3a. ***phellos*** subsp. ***phellos*** (v) 'diversicaule' (p. 25)
Leaves narrowly elliptic to oblong, spreading or becoming ascending 3a. ***phellos*** subsp. ***phellos*** (vi) 'tamanum' (p. 25)

22(8) Inflorescence-branching cymose; leaves always broadest at or below middle, rarely petiolate, with margin plane or incurved, not minute and scale-like 23
Inflorescence-branching pseudo-dichotomous or lateral; leaves broadest below to above middle, often petiolate, with margin plane or recurved or, if incurved, then minute and scale-like 37

23(22) Leaves plane, oblong, with 3–7 basal veins becoming deflexed when withering; sepals 6–11 mm long 24

Leaves incurved or involute or conduplicate, or if plane then broadly ovate or 1-nerved, becoming deflexed or not; sepals 2–6(–7) mm long 25

24(23) Leaves smooth, ± lustrous, the pairs very shortly united; stigmas narrow ... 10. **simonsii** (p. 34)
Leaves papillose, dull, the pairs united to form a cup-shaped sheath; stigmas capitate 11. **papillosum** (p. 34)

25(23) Leaves united only by interfoliar ridge, not becoming deflexed (except sometimes 12. *lycopodioides*) 26
Leaves with bases of lamina united, often becoming deflexed 32

26(25) Leaves with midrib proximally prominent or wholly level with lamina; lamina conduplicate, apex usually acuminate to obtuse 27
Leaves with midrib proximally impressed; lamina incurved, apex usually obtuse to rounded 28

27(26) Leaves coriaceous, markedly tetrastichous, apex acuminate to acute, margin plane 12. **lycopodioides** (p. 36)
Leaves chartaceous, weakly or not tetrastichous, apex acute to rounded, margin usually undulate .... 13. **thuyoides** (p. 37)

28(26) Leaves sessile, elliptic-oblong to narrowly oblong, base cuneate to parallel 29
Leaves shortly petiolate or base angustate, if base narrowly cuneate, then lamina linear to acicular 30

29(28) Leaves 5–7 mm long, elliptic or oblong to obovate; sepals 1·8–2·3 mm wide, apex plane 22. **hartwegii** (p. 51)
Leaves 2–4 mm long, narrowly elliptic or narrowly oblong to linear; sepals 0·7–1·7 mm wide, apex incurved-cucullate .... 23. **maguirei** (p. 52)

30(28) Leaves subpapillose beneath, base cuneate to pseudopetiolate; sepals obtuse to rounded 19. **sabiniforme** (p. 45)
Leaves smooth beneath, base narrowly cuneate to angustate or parallel-sided; sepals acute to obtuse 31

31(30) Plant a bushy or spreading shrub or small tree (0·1)0·3–6 m tall; leaves with glands not or scarcely impressed; sepals usually plane .... 20. **laricifolium** (p. 47)
Plant a pulviniform shrub 0·08–0·16 m tall; leaves with glands impressed; sepals markedly ribbed .... 21. **martense** (p. 51)

32(25) Flowers 18–40 mm in diam.; leaf base rounded to cordate-amplexicaul 33
Flowers 6–12 mm in diam.; leaf base parallel to truncate 35

33(32) Stem internodes smooth; leaves plane or slightly saccate, (2–)3–7 mm wide, margin not or scarcely hyaline .... 16. **cuatrecasii** (p. 41)
Stem internodes with corky emergences, at least below upper leaves; leaves saccate or incurved-cucullate, 0·7–3·5 mm wide, margin markedly hyaline 34

34(33) Leaves becoming reflexed, saccate; sepals 5–8 mm wide .... 14. **goyanesii** (p. 38)
Leaves spreading only, incurved-cucullate; sepals 4–5 mm wide ..... 15. **myricariifolium** (p. 40)

35(32) Leaves becoming deflexed, broadly ovate to triangular-ovate or (lower) oblong, basal veins 3(5) .... 17. **quitense** (p. 41)
Leaves at most spreading only, triangular-ovate or oblong to linear, basal veins 1(3–5) (18. **loxense**) 36

36(35) Leaves broadly triangular-ovate to lanceolate, usually imbricate, base truncate to broadly cuneate .... 18a. **loxense** subsp. **aequatoriale** (p. 44)
Leaves narrowly oblong or narrowly elliptic to oblanceolate or linear, usually spreading, base narrowly cuneate to parallel .... 18b. **loxense** subsp. **loxense** (p. 45)

37(22) Leaves with parallel venation (5–7-veined); flowers 3–12 in condensed cyme; shrub 61. **cymobrathys** (p. 103)
Leaves with pinnate venation or 1-nerved; flowers ∞ in ± lax cymes; suffrutices or herbs [62–80. See Part 8]

38(5) Leaf venation parallel (5–7-veined), veins unbranched; flowers 3–12 in condensed cyme 61. **cymobrathys** (p. 103)
Leaf venation flabellate or pinnate or 1-nerved, veins branched or not; flowers solitary (except in 26. *mexicanum*) 39

39(38) Leaves and usually sepals ± markedly incurved-cucullate; leaves distally broadened, not linear 40
Leaves plane to incurved; leaf and sepal apices not cucullate or, if so, then lamina narrowly elliptic or narrowly oblong to linear 45

40(39) Leaves with margin viscid, usually obovate; flowers often in dense cymes; stigmas ± capitate 41
Leaves with margin not viscid, broadly elliptic to obovate-spathulate; flowers solitary; stigmas narrow or, if capitate then leaves oblanceolate 42

41(40) Flowers solitary, 20–40 mm in diam., sometimes terminating clustered short shoots; leaves 7–10 mm long, always coriaceous; habit erect .... 25. ***gleasonii***(p. 55)
Flowers in 3–13-flowered cymes or, if solitary, less than 20 mm in diam.; leaves up to 17 mm long, sometimes chartaceous and then habit decumbent and rooting
26. ***mexicanum***(p. 56)

42(40) Leaves elliptic-ovate to elliptic-lanceolate, 3–7 mm broad venation flabellate; flowers 25–40 mm in diam. .... 27. ***stuebelii***(p. 58)
Leaves oblanceolate to narrowly oblong, 0·7–3 mm broad, venation pinnate or 1-nerved; flowers 6–25 mm in diam. (petals unknown in 28. *prietoi*) 43

43(42) Sepals acuminate; leaves persistently imbricate-tetrastichous, markedly laterally compressed distally; stigmas capitate .... 28. ***prietoi***(p. 58)
Sepals acute; leaves eventually outcurving, not laterally compressed distally or, if so (29. *cassiopiforme* in part) then stigmas narrow 44

44(43) Petals *c.* 14 mm long; styles longer than ovary; stigmas narrow; leaves oblanceolate (l: b = *c.*2.5) .... 29. ***cassiopiforme***(p. 59)
Petals 5–9 mm long; styles 0·6–1 × as long as ovary; stigmas capitate; leaves narrowly oblanceolate to linear-elliptic (l: b = 4–11) .... 30. ***decandrum***(p. 59)

45(39) Leaves with venation flabellate, some laterals free or almost free from the base; styles stout with stigma usually capitate .... 31. ***pimeleoides***(p. 60)
Leaves with venation pinnate, all laterals originating well above the base; styles and stigmas various 46

46(45) Leaves petiolate or abruptly narrowed at the base; stem sometimes apparently articulated 47
Leaves sessile, gradually narrowed or parallel-sided at the base; stem not articulated 54

47(46) Styles 6–7 mm long; flowers 25–30 mm in diam.; leaves often spreading abruptly above petiole .... 49. ***jaramilloi***(p. 86)
Styles 0·8–5 mm long; flowers up to 25 mm in diam.; leaves outcurving or spreading from the base 48

48(47) Leaves with midrib prominent or level with lamina beneath, glands usually visible beneath 49
Leaves with midrib ± impressed beneath, glands not visible beneath 53

49(48) Stigmas ± broadly capitate; leaves glaucous, dull .... 50. ***cardonae***(p. 87)
Stigmas clavate or small; leaves not glaucous, ± lustrous 50

50(49) Leaves with margins recurved (51. ***caracasanum***) 51
Leaves with margin or whole lamina incurved 52

51(50) Leaves 9 × 4–5 mm or larger; petals *c.* 1·3 × as long as sepals; styles *c.* 1·3 × as long as ovary
51a. ***caracasanum*** subsp. ***caracasanum***(p. 89)
Leaves 8 × 3·5 mm or smaller; petals 1·5–2 × as long as sepals; styles 2–2·5 × as long as ovary .... 51b. ***caracasanum*** subsp. ***turumiquirense***(p. 90)

52(50) Leaf lamina elliptic, 2–4 mm wide, plane with margin incurved; styles 5–6 mm long
52. ***ekmanii***(p. 90)
Leaf lamina narrowly elliptic to linear, 0·5–2 mm wide, incurved to canaliculate; styles 3·5–4 mm long .... 53. ***pycnophyllum***(p. 92)

53(48) Leaves plane or with margin subincrassate, narrowly ovate to narrowly oblong-elliptic; sepals 1·5–4 mm wide; styles 2·5–4 mm long .... 55. ***ruscoides***(p. 93)
Leaves incurved to canaliculate, very narrowly lanceolate to (usually) linear; sepals 0·5–1·5 mm wide; styles 1–2(–3) mm long .... 59a. ***lancioides*** subsp. ***lancioides***(p. 99)

54(46) Leaf and sepal apices ± incurved-cucullate; leaf lamina narrowly oblong or narrowly elliptic to linear, narrowed at the base 55

Leaf and sepal apices not incurved or cucullate or, if so, then leaves broadened at the base 60

55(54) Ovary ellipsoid to globose; styles 0·8–2(–3) mm long, 0·4–1·1 × as long as ovary, stigmas ± broadly capitate; sepals usually oblong to oblanceolate, not ribbed 56
Ovary ovoid; styles *either* 3–4·5 mm long, 1·3–1·5 × as long as ovary, stigmas scarcely to narrowly capitate, *or* if styles shorter (1·5–2·5 mm long, 0·6–0·7 × as long as ovary) and broadly capitate, then sepals lanceolate, ± ribbed 58

56(55) Stems erect or rarely decumbent; leaves 7–15 mm long; sepals 5–8 mm long; styles 3(4), 1–2(–3) mm long (59. ***lancioides***) 57
Stems prostrate or ascending; leaves 4–7 mm long; sepals 3–4 mm long; styles (3)4–5, 0·8–1 mm long ..... 60. ***selaginella*** (p. 102)

57(56) Flowers terminal, solitary, inflorescence-branching pseudo-dichotomous; habit bushy or caespitose ..... 59a. ***lancioides*** subsp. ***lancioides*** (p. 99)
Flowers terminal and lateral in dense racemiform heads; habit bushy or straggling ..... 59b. ***lancioides*** subsp. ***congestiflorum*** (p. 101)

58(55) Styles 3–4·5 mm long, 1·3–1·5 × as long as ovary; stigmas not or scarcely capitate; leaves 1·5–4 mm wide, margin not or scarcely hyaline 59
Styles 1·5–2·5 mm long, 0·6–0·7 × as long as ovary; stigmas broadly capitate; leaves 0·8–1·5 mm wide, margin narrowly but distinctly hyaline ..... 58. ***andinum*** (p. 97)

59(58) Sepals oblong-oblanceolate, not ribbed; leaves plane or with margin slightly incurved, 6–9 mm long, markedly tetrastichous, glaucous ..... 56. ***ilanganaticum*** (p. 95)
Sepals ovate-lanceolate to oblong, ribbed; leaves with margin markedly incurved, 8–15 mm long, not or obscurely tetrastichous, lustrous ..... 57. ***struthiolifolium*** (p. 96)

60(54) Styles 6–7·5 mm long; flowers 20–30 mm in diam.; leaves with midrib branched, lamina elliptic to oblanceolate, plane or conduplicate, epidermis smooth 32. ***magdalenicum*** (p. 63)
Styles up to 5 mm long; flowers up to 20 mm in diam.; leaves with midrib unbranched or, if branched, then lamina narrowly oblong or epidermis papillose above 61

61(60) Leaves markedly tetrastichous, narrowly elliptic, papillose above; branches very strict, parallel, with internodes 1–1·5 mm long ..... 43. ***parallelum*** (p. 76)
Leaves not tetrastichous or if so, then linear, smooth, and branches not as above 62

62(61) Sepal margin green or, if hyaline, then inflorescence a racemiform synflorescence and styles shorter than ovary with stigmas capitate 63
Sepal margin hyaline; inflorescence and styles not as above 72

63(62) Flowers solitary, not congested; styles 2·5–5 mm long, stigmas narrow 64
Flowers in ± congested heads or racemiform synflorescences; styles 1–3(4·5) mm long, stigmas ± broadly capitate 70

64(63) Leaves 2–3 mm wide, narrowly elliptic, slightly incurved ..... 33. ***valleanum*** (p. 64)
Leaves 0·4–2 mm wide, very narrowly oblanceolate to linear, markedly incurved to conduplicate 65

65(64) Styles 2·5–3·5 mm long; leaves lustrous beneath 66
Styles 1–2 mm long; leaves dull beneath 69

66(65) Leaves becoming twisted, incurved but not carinate or conduplicate, margin very narrowly hyaline, dorsally usually glandular when mature 67
Leaves remaining erect or becoming recurved, incurved to conduplicate, often at least partly carinate, margin broadly hyaline, dorsally eglandular when mature 68

67(66) Sepals 7–11 mm long; flowers 20–30 mm in diam.; capsule *c.*5 mm long; leaves 6–12 × 0·8–1·7 mm; stamens 60–75 ..... 34. ***sprucei*** (p. 65)
Sepals 4–7 mm long; flowers 10–18 mm in diam.; capsule 3·5–4 mm long; leaves 3·7–7 × 0·4–0·6 mm; stamens 30–55 ..... 35. ***aciculare*** (p. 66)

68(66) Leaves imbricate at first but not markedly tetrastichous, recurving, 5–8 mm long; flowers 15–20 mm in diam.; petals 8–12 mm long ..... 39. ***recurvum*** (p. 68)
Leaves densely and persistently imbricate, 'winged'-tetrastichous, scarcely spreading, 9–14 mm long; flowers 20–25 mm in diam.; petals 15–18 mm long..... 40. ***wurdackii*** (p. 69)

69(65) Flowers 15–20 mm in diam.; leaves 5–15 mm long, acute; stems woody, not rooting
38. ***costaricense*** (p. 70)

Flowers 6–8 mm in diam.; leaves 3–5 mm long, subacute to obtuse; stems wiry, basally rooting ..... 39. ***bryoides*** (p. 71)

70(63) Leaves very narrowly elliptic, 15 × 3 mm or larger; sepals 9–11 mm long, coriaceous; styles *c.*4·5 mm long ..... 40. ***bolivaricum*** (p. 72)

Leaves linear, up to 14 × 1·5 mm; sepals 2–7 mm long, chartaceous to membranous; styles 0·6–3 mm long 71

71(70) Stems erect to decumbent; leaves 6–14 mm long; styles 1·5–3 mm long, longer than ovary 41. ***juniperinum*** (p. 72)

Stems prostrate; leaves 2–5 mm long; styles 0·6–0·8 mm long, shorter than ovary 42. ***prostratum*** (p. 75)

72(62) Leaves lustrous, margin markedly incurved, lamina twisting and sometimes recurving (44. ***marahuacanum***) 73

Leaves dull or with metallic sheen, margin plane to incurved, lamina recurving only 75

73(72) Stigmas small or slightly enlarged; ovary and capsule acute; inflorescence branching pseudo-dichotomous or racemiform 74

Stigmas enlarged to capitate; ovary and capsule ± rostrate, inflorescence branching pseudo-dichotomous to lateral-congested 44c. ***marahuacanum*** subsp. ***chimantaicum*** (p. 80)

74(73) Styles 4–5 mm long; sepals 7–9 mm long; inflorescence branching pseudo-dichotomous 44a. ***marahuacanum*** subsp. ***marahuacanum*** (p. 79)

Styles 2–3(–4) mm long; sepals 4–6 mm long; inflorescence branching lateral, ± racemiform ..... 44b. ***marahuacanum*** subsp. ***strictissimum*** (p. 79)

75(72) Leaves plane or slightly incurved, oblong to oblong-linear or narrowly oblanceolate, the tips not red when young ..... 45. ***lancifolium*** (p. 80)

Leaves markedly incurved to canaliculate, linear to linear-acicular, the tips usually red when young 76

76(75) Plant a prostrate shrublet with branches matted, rooting; leaves often secund, not tetrastichous ..... 46. ***horizontale*** (p. 81)

Plant an erect shrub with branches strict, not rooting; leaves never secund, usually ± tetrastichous 77

77(76) Leaves with metallic sheen, markedly tetrastichous, erect to suberect 47. ***tetrastichum*** (p. 82)

Leaves dull, not tetrastichous (except sometimes in young parts or plants); usually outcurving (48. ***strictum***) 78

78(77) Leaf and sepal apices acicular; sepals 1·3–2 mm wide, not ribbed; leaves 8–13 mm long; branches strict, usually all from one stem ..... 48a. ***strictum*** subsp. ***strictum*** (p. 84)

Leaf and sepal apices subacute; sepals 1–1·2 mm wide, clearly ribbed; leaves 5–7(8) mm long; branches ascending, usually branched from the base 48b. ***strictum*** subsp. ***compactum*** (p. 85)

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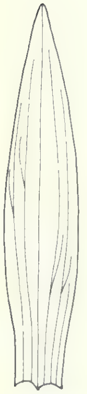

1. **Hypericum terrae-firmae** Sprague & Riley

in *Kew Bull.* **1924**: 12 (1924). Type: Belize, without precise locality, 1912? (fr), *Peck* 321 (K!, holotype; GH!, isotype).

H. styphelioides sensu Standley & Williams in *Fieldiana Bot.* **24** (7): 51 (1961); P. Adams in *Rhodora* **64**: 236 (1962), non A. Richard (1845).

Icon: Fig. 4.

Shrub or small tree, 1–2 m tall, erect, with branches strict, pseudo-dichotomous or lateral. *Stems* orange-brown, 4-lined when young, soon terete, without corky wrinkles, cortex exfoliating in strips; internodes 4–6 mm long. *Leaves* sessile, free from the base, spreading to subimbricate and tetrastichous, deciduous at the base without fading; lamina 16–30 × 4–6 mm, narrowly oblong to narrowly elliptic, plane, not cucullate or carinate, concolorous, not or slightly glaucous, chartaceous to thinly coriaceous; apex acute, base narrowly cuneate to subangustate, not sheathing,

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* The leaves and petals in the marginal text figures are all respectively twice and one-and-a-half times natural size. In the inflorescence diagrams ○ = open flower, ● = flower bud, × = vegetative bud, ↑ = continuing shoot.
Note. In part 3 (Robson, 1985) the magnifications in the legends to figs 9–24 should all have been reduced by half.

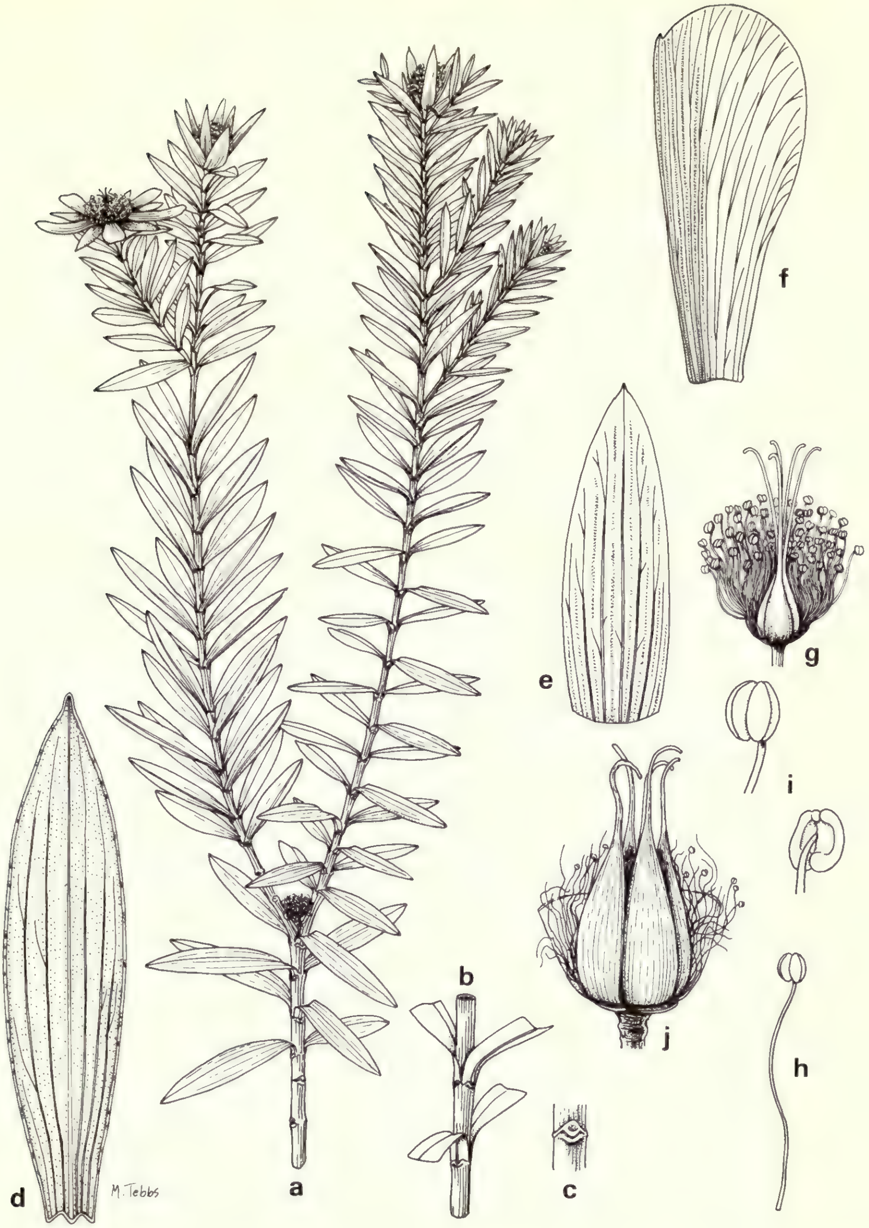
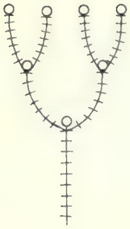
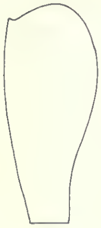


Fig. 4 *H. terrae-firmae*: (a) habit; (b) stem with leaf bases; (c) leaf scar; (d) leaf; (e) sepal; (f) petal; (g) stamens (partly cut away) and ovary; (h) stamen; (i) anthers; (j) capsule (a, b = ½; c × 1; d, j × 2; e–g × 3; h × 8; i × 15). (a–d, g, j) *Hunt* 66; (e, f, h, i) *Sutton et al.* 193.

pairs free; basal veins 7, subparallel-sided, with short lateral branches, tertiary reticulation not visible; laminar glands dense, not prominent. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from 1–2 nodes below; pedicel absent or very short; upper leaves transitional. *Flowers* 40–60 mm in diam., stellate. *Sepals* 14–22 × 3–7 mm, narrowly oblong, acute; veins 15, dichotomising and reticulate distally, with midrib prominent; glands linear. *Petals* bright yellow, 20–30 × 7–12 mm, *c.* 1·3 × sepals, oblanceolate; apiculus acute; glands linear, mostly uninterrupted. *Stamens c.* 250, longest 9–11 mm long, *c.* 0·3–0·4 × petals. *Ovary* (2·5–)3



–4·5 × 2–2·5 mm, ± narrowly ovoid; styles 5, 5–7 mm long, 1·4–3 × ovary, erect, outcurved below apex; stigmas small. *Capsule* 8–10 × 5–7 mm, broadly ovoid, shorter than sepals. *Seeds* c. 1 mm long, not or shallowly carinate; testa finely scalariform-reticulate.



In open pine or oak-pine forest or pine savannah on granite, often near streams; lowland to 550 m.

Belize (Cayo, Belize). Map 1.

BELIZE. Belize: Colonel English Pine Ridge, Belize-Cayo road, 20.i.1958 (fl), *Gentle* 9515 (DUKE, F, NY, S, US); Burrellboom, *c.* 9 m, 22.iii.1970 (fr), *McDaniel* 12853 (F). Cayo: Mountain Pine Ridge, San Miguel, 400 m, 2.vi.1979 (fl & fr), *Whitefoord* 1935 (BM); Mountain Pine Ridge, Augustine, vii–viii.1936 (fl), *Lundell* 6617 (F, K, MICH, NY, US).

H. terrae-firmae, as previous authors have pointed out, is closely related to the Cuban *H. styphelioides*, especially to forms of subsp. *clarense*; but the thinner, longer, acute leaves, which spread more or less widely from the base, and the large flowers with longer, narrowly oblong sepals, allow the Belize plant to be accorded specific rank. Its nearest ancestral taxon is in East Africa (*H. revolutum* subsp. *keniense* (Schweinfurth) N. Robson), a subspecies of Sect. 1 *Campylosporus*.

2. **Hypericum styphelioides** A. Richard

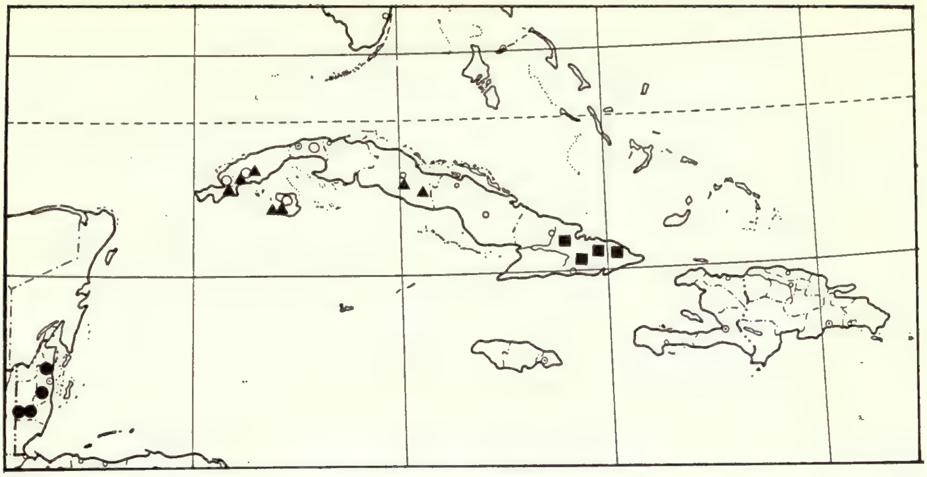
in Sagra, *Hist. Phys., Pol. Nat. Ile Cuba* (Bot. – Pl. Vasc.): 237 (1845); León & Alain, *Fl. Cuba* **3**: 316, t. 141 (1953); Lippold in *Wiss Z. Friedr.-Schiller Univ. Jena* (Math.-Nat. R.) **19**: 378, f.2. (1970). Type: Cuba, [Pinar del Rio, near San Diego de los Baños], *Sagra* s.n. (P, holotype).

Shrub 0·15–2 m tall, erect, with branches erect, strict, pseudo-dichotomous or lateral. *Stems* orange-brown, 4-lined when young, soon terete, without epidermal wrinkles, cortex exfoliating in strips or scales; internodes 2–6 mm long. *Leaves* sessile, spreading from above the base to closely imbricate and tetrastichous, deciduous at the base without fading; lamina 5–25 × 2–8 mm, narrowly obovate to narrowly elliptic or narrowly oblong, plane or incurved, sometimes ± concave, not carinate, concolorous, lightly to densely glaucous, thinly to thickly coriaceous; apex shortly acuminate to acute, base cuneate to scarcely angustate, not or slightly sheathing, pairs free; basal veins 5–9(–11), subparallel to flabellate, branching distally to form a lax reticulum, tertiary reticulum not visible; laminar glands dense, ± prominent. *Inflorescence* 1(2)-flowered, with pseudo-dichotomous branches from 1–2 nodes below, sometimes with additional branches from immediately lower node; pedicel absent or very short; upper leaves transitional. *Flowers* 15–50(–70) mm in diam., stellate. *Sepals* 5–15 × 2–5 mm, oblong or lanceolate to obovate, acute or obtuse-apiculate to obtuse; veins 5–17, dichotomising, and reticulating distally, with midrib prominent beneath; glands linear, sometimes distally punctiform. *Petals* bright yellow, (8–)10–22 × 2–10 mm, *c.* 1·5 × sepals, oblanceolate; apiculus acute; glands linear, uninterrupted. *Stamens* c. 70–200, longest 5–9 mm long, *c.* 0·3–0·5 × petals. *Ovary* 2–4 × 1·5–3 mm, ovoid to rostrate-subglobose; styles (4)5, 3–5 mm long, 1·2–1·5 × ovary, erect, outcurved below apex; stigmas small. *Capsule* (3–)4–8 × 2–7 mm, ovoid-subglobose, shorter than sepals. *Seeds c.* 1 mm long, not or shallowly carinate; testa finely scalariform-reticulate.

In pine forest or pine savannah or often on sterile white sands, especially round margins of lakes and pools; 0–800 m.

Cuba (Pinar del Rio, Las Villas, Oriente, Isla de Pinos). Map 1.

Three subspecies of *H. styphelioides* have been recognized. Subsp. *clarense*, the most similar to *H. terrae-firmae*, has a disjunct distribution (central Cuba, western Cuba, Isla de Pinos), whilst the others are respectively eastern (subsp. *moaense*) and western (subsp. *styphelioides*).



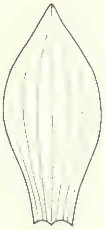
Map 1 1. *H. terrae-firmae* ●. 2. *H. styphelioides*: a. subsp. *clarense* ▲, b. subsp. *styphelioides* ○, c. subsp. *moaense* ■.

2a. **Hypericum styphelioides** subsp. **clarense** Lippold

in *Wiss. Z. Friedr.-Schiller Univ. Jena* (Math.-Nat. R.) **19**: 379, f. 2. (1970). Type: Cuba, Las Villas, Santa Spiritus, Rio Gayabo, 7.xii.1911 (fl), *Bro. Clemente* 2884 (LS, holotype; NY!, isotype).

Hypericum incurvum Urban, *Symb. Antill.* **9**: 405 (1925); León & Alain, *Fl. Cuba* **3**: 317 (1953); Lippold in *Wiss. Z. Friedr.-Schiller Univ. Jena* (Math.-Nat. R.) **19**: 380, f. 2. (1970). Type: Cuba, Isla de Pinos, Santa Barbara, Westport, 3.xii.1920 (fl), *Ekman* 12072 (S!, holotype).

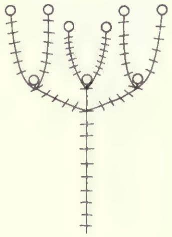
Shrub 0·15–0·6(–1) m tall. *Leaves* 10–18 × 2–5·5 mm, narrowly elliptic to narrowly oblong, thinly to thickly coriaceous, not or lightly glaucous, plane to concave or incurved, spreading or outcurving; apex acute; basal veins 5(7). *Flowers* 15–30 mm in diam. *Sepals* oblong to lanceolate, acute or obtuse, 5-veined; glands prominent. *Petals* 7–16 mm long. *Styles* 5, 3–5 mm long.



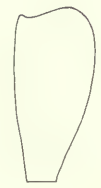
Savannahs, fields, and coastal sands, sometimes on weathered dolomite; lowland to montane.

In Las Villas, western Pinar del Rio and Isla de Pinos.

CUBA. Pinar del Rio: N. of San Diego de los Baños, 13.iv.1900 (st), *Palmer & Riley* 535 (NY, US); mountains near El Guama, 6.iii.1900 (fr), *Palmer & Riley* 160 (NY, US). Las Villas: Lomas de Banao, i.1920 (fl), *Lund* 123 (NY); Trinidad Mts, Buenos Aires, near La Sabana, 5.viii.1936, *Smith, Hodgson & Gonzales* 3381 (F, NY, S, US). Isla de Pinos: Siguanea, 26.ii.1916 (fl), *N. L. Britton, E. G. Britton & Wilson* 14926 (F, NY, S, US); between Mine de Oro and Playa del Soldado, 12.i.1956, *Killip* 45389 (US).



Subsp. *clarense* forms a cline from eastern Las Villas (where the flowers are larger and the leaves are broader and flat) via eastern Pinar del Rio to Isla de Pinos (where the flowers are smaller and the leaves narrow with an incurved margin and outcurving towards the apex).



2b. **Hypericum styphelioides** A. Richard subsp. **styphelioides**

Shrub 0·3–2 m tall. *Leaves* 8–25 × 4–8 mm, oblanceolate to narrowly obovate, plane, ± densely glaucous, ± thickly coriaceous, spreading to densely imbricate; apex shortly acuminate; basal veins 7–9(–11); glands not usually prominent. *Flowers* 15–50(–70) mm in diam. *Sepals* elliptic to obovate, acute or obtuse-apiculate to obtuse, 9–17-veined. *Petals* 10–22 mm long. *Styles* 5, 3–5 mm long.

In pine forest or savannah sand or in wet places; lowland.

In Isla de Pinos, Las Villas and Pinar del Rio.
CUBA. Pinar del Rio: El Sábalo, Finca Sabanalamar, near sea level, 22.xiii.1937 (fl), *Killip* 32263 (NY, US); Herradura, 1904 (fl), *van Hermann* 562 (BM, F, K, NY, P, US); near Laguna Alcatraz Grande, 16.xii.1911 (fl), *Shafer* 11016 (NY, US). Las Villas: Banao Mts., Sabana de la Gloria, 29.vii.1918 (fl), *Léon & Roca* 7928 (NY). Isla de Pinos: San Pedro and vicinity, 12.ii.–22.ii.1916 (fl), *N. L. Britton, E. G. Britton & Wilson* 14148 (F, NY, S, US); Los Indios, 4.ii.1953 (fl), *Killip* 42603 (NY, US).

Subsp. *styphelioides* forms two incompletely correlated clines eastward, showing reduction in size and increasing leaf-imbrication. The only specimen seen from Las Villas (*Léon & Roca* 7928) is somewhat intermediate between subsp. *styphelioides* and subsp. *moaense*.

2c. **Hypericum styphelioides** subsp. **moaense** Lippold

in *Wiss. Z. Friedr.-Schiller Univ. Jena* (Math.-Nat. R.) **19**: 379, f.2 (1970). Type: Cuba, Oriente, Plano el Sierra de Moa, *Bisse* 11676 (JE, holotype; HAJB, isotype).

Shrub 0·6–1·5 m tall. *Leaves* 7–11(–16) × 2–6 mm, obovate (or rarely oblanceolate) to narrowly elliptic, thickly coriaceous; slightly glaucous, ± cucullate or incurved, usually ± densely imbricate; apex apiculate-obtuse to acute; basal veins 5–7; glands prominent. *Flowers* 15–20 mm in diam. *Sepals* lanceolate, acute, 7-veined. *Petals* 8–12 mm long. *Styles* 5(4), *c.* 3 mm long.

In pine woods and open, dry or marshy habitats, on laterite or serpentine soils; 0–800 m.

Confined to Oriente.
CUBA. Oriente: Minas de Iberia, Taco Bay, in mountains, *c.* 800 m, 7–8.xii.1914 (fl), *Ekman* 3787 (F, K, MICH, NY, S); Moa, near airfield, vii.1941 (fl), *Howard* 6020 (BM, NY, P, S, US); Maraví (near Barancoa), 25.xii.1914 (st), *Ekman* 4020 (NY, S, US).

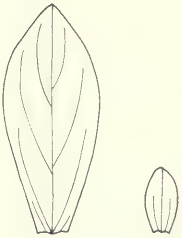
*The **H. phellos** group (Spp. 3–9)* Fig. 1, p. 4

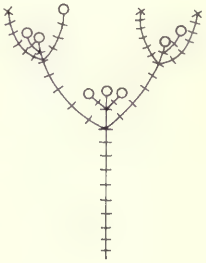
The most primitive form of 3 *H. phellos* has relatively large, marcescent leaves as in 10 *H. simonsii*. In the other forms of the species, however, the leaves are either (i) smaller and more rigid, deciduous at the apparent base or persisting, or (ii) narrower and more revolute, deciduous at the apparent base only after drooping but not withering. The extreme variability of *H. phellos* in a relatively restricted area, together with the absence of clear morphological disjunctions, makes it difficult to recognize infraspecific taxa in this species and to differentiate it from its nearest relatives. The form with marcescent leaves (3a subsp. *phellos* (i) 'marcescens') differs from *H. simonsii* in having leaves free at the base with the apex acute to acuminate and the margin recurved, as well as rounded sepals; but it intergrades with both the form having thicker, narrow, drooping leaves with recurved margins and densely corky internodes (13a subsp. *phellos* (ii) 'angustum') and the form with smaller, chartaceous, spreading leaves, also with recurved margins, but with an acuminate apex and sometimes only slightly corky internodes (3a *phellos* subsp. *phellos* (v) 'diversicaule'). From (ii) 'angustum' two distinct trends are apparent in subsp. *phellos*: to (iii) 'patens', in which the leaves are thicker with more recurved margins and usually fall when spreading or soon after becoming appressed, and to (iv) 'phellos' (including the type), in which the leaves are narrower and become markedly appressed but not so thick. Variant (ii) 'patens' gives rise to the *H. garciae* group (Spp. 4–6), with narrow revolute leaves, as well as 3b *H. phellos* subsp. *oroqueanum*, with narrow continually appressed leaves, and 7 *H. irazuense* (Costa Rica), whilst the (iv) 'phellos' trend continues to 8 *H. stenopetalum*, which has a distribution overlapping that of *H. phellos*. On the other main division of *H. phellos* subsp. *phellos*, (v) 'diversicaule' is related to 9 *H. carinosum*, which has smaller, 1-nerved leaves and smaller flowers, whereas (vi) 'tamanum', which differs from 'diversicaule' only in its relatively broader and more obtuse leaves and sepals and more clearly differentiated lateral shoots, gives rise to a high-altitude condensed form (3c subsp. *platyphyllum*) in which the leaves become incurved and remain appressed until they are shed.

3. **Hypericum phellos** Gleason

in *Bull. Torrey bot. Club* **56**: 106 (1929). Type: Colombia, Santandér, Páramo de la Puentes, above La Baja, 3700–3800 m, 25.i.1927 (fl), *Killip & Smith* 18199 (NY!, holotype; F!, GH!, K!, US! isotypes).

Shrub or small tree 0·3–4 m tall, erect, with branches strict, almost always lateral. *Stems* yellow-brown, 4-lined and ± ancipitous when young, becoming terete, often with transverse epidermal or corky wrinkles or emergences immediately below the node or ± throughout the internode, cortex exfoliating in strips; internodes 1·5–3 mm long. *Leaves* sessile, spreading from the base or imbricate and tetrastichous, deciduous near the base after fading or persistent; lamina 4–20 × (1–)2–6 mm, narrowly to broadly elliptic or oblong to obovate or oblanceolate, plane or recurved, not concave, not or scarcely carinate, concolorous, not glaucous, thickly to thinly coriaceous; apex shortly acuminate to rounded, base cuneate to angustate, not sheathing, free or pairs united to form a narrow interfoliar ridge; basal veins 3–7, diverging, all or only the midrib branching, tertiary reticulation obscure or not visible; laminar glands rather dense, impressed above, ± prominent beneath. *Inflorescence* 1(2–5)-flowered, terminal and on short lateral shoots, with extension shoots usually from 2–3 nodes below; peduncle and pedicels 1–9 mm long; upper leaves foliose or bracteose. *Flowers* 15–30 mm in diam., stellate. *Sepals* 4–9 × 1·5–3 mm, ± narrowly oblong to lanceolate or elliptic or rarely oblanceolate, acute or acuminate to obtuse or rarely rounded; veins 5–7, branched distally, midrib not or scarcely prominent; glands mostly linear or up to half punctiform. *Petals* bright yellow to orange-yellow, sometimes margined red, 8–15 × 4–8 mm, *c.* 2 × sepals, oblanceolate to narrowly obovate; apiculus acute; glands all linear or distally interrupted. *Stamens c.* 40–200, longest 5–8 mm long, *c.* 0·5–0·7 × petals. *Ovary* 2–3·5 × 1·5–2 mm, ovoid; styles 3, (5–)6–9 mm long, 2–3 × ovary, spreading, incurved distally; stigmas small or subcapitate. *Capsules* 4–5·5 × 3·5–5 mm, subglobose to globose, shorter than sepals. *Seeds c.* 1 mm long, ecarinate; testa finely scalariform.

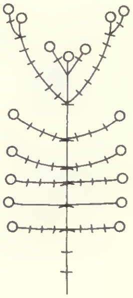




On scrubby slopes and in moist woods immediately below them; 2600–4200 m.

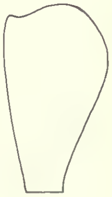
Colombia (Santandér, Norte de Santandér, César), Venezuela (Táchira). Map 2.

Hypericum phellos can be distinguished from its nearest relatives only by a combination of characters. Nearly always the stem internodes have corky ridges or emergences, especially below the node, and the leaves are deciduous. Where they are persistent, they are either marcescent with apex acute ('marcescens') or broad and remaining appressed, thus apparently preventing the development of the corky emergences (subsp. *platyphyllum*). The other recognizable subspecies (subsp. *oroqueanum*) has leaves that remain appressed but eventually fall.

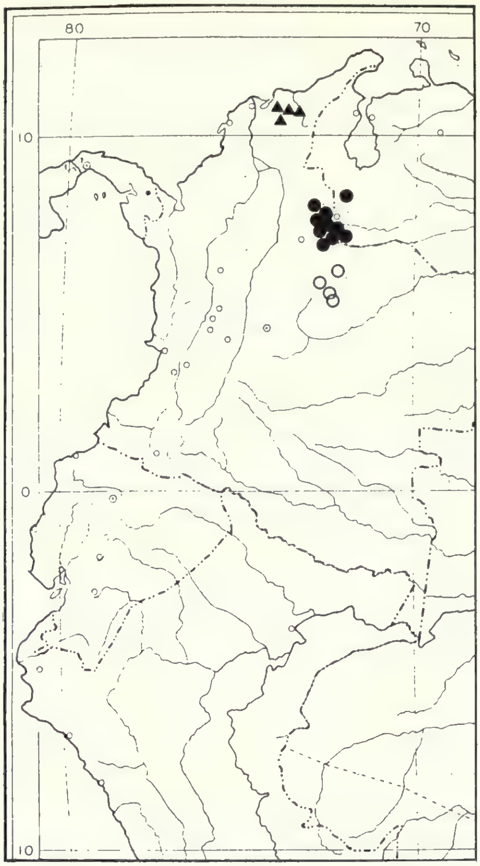


3a. **Hypericum phellos** subsp. **phellos**

H. tamanum Cuatrec. in *Ciencia Mex.* **4**: 65 (1943). Type: Colombia, Norte de Santandér, Páramo de Tamá, vicinity of La Cueva, 3100–3200 m, 27.x.1941 (fl), *Cuatrecasas, Schultes & Smith* 12647 (COL, holotype; BM!, F!, U!, US!, isotypes).
H. thymifolium Cuatrec. in sched., non Kunth.
H. tachirense Steyerm. in sched.



Shrub or small tree 0·3–4 m tall, with shoots rounded to pyramidal or narrowly cylindric, not or ± markedly differentiated into elongate main stems and short laterals; internodes with slight or pronounced corky emergences. *Leaves* free,



Map 2 3. *H. phellos* (all subspecies) ●; 10. *H. simonsii* ▲; 11. *H. papillosum* ○.

spreading then deciduous directly or after decurving or after deflexing and withering; lamina 5·5–16 × 1·4–7 mm, oblanceolate to elliptic or oblong, acute to acuminate, margin recurved to plane. *Sepals* 4–9 × 2–3 mm, narrowly oblong or elliptic to lanceolate or ovate-lanceolate. *Petals* 10–15 × 4–8 mm. *Stamens* c. 40–200. *Styles* 5–9 mm long.

Colombia (Norte de Santandér, Santandér), Venezuela (Táchira); 2500–3900 m.

COLOMBIA. Norte de Santandér: Páramo de Fontibón, 2600–2750 m, 15–16.x.1941 (fl), *Cuatrecasas, Schultes & Smith* 12298 (BM, COL, GH, NY, U, US); between Mutíscua and Pamplona, 3400 m, 23.ii.1927 (fl), *Killip & Smith* 19727 (GH, S, US); Hoya del Rio Chitagá, Quebrada de Presidente, 3100–3300 m, 28.xi.1941 (fl), *Cuatrecasas* 13490 (COL, NY). Páramo de Tamá, vicinity of the Cueva, 3100–3200 m, 27.x.1941 (fl), *Cuatrecasas, Schultes & Smith* 12647 (BM, F, US). Santandér: Páramo de Santurbán entre Bucaramanga & Berlin, W. side, *c.* 3200 m, 3.i.1960 (fl & fr), *Barclay & Juajibioy* 10422 (NY); Berlin to Picacho, 3058 m, 14.viii.1977 (fl), *Renteria, Mantilla, Niño & Ortiz* 555(3) (COL, MO); vicinity of La Baja, 2700 m, 14–31.i.1927, *Killip & Smith* 18756 (GH, NY, US).

VENEZUELA. Táchira: Páramo de Batallón, near La Grita, 3100 m, 8.iii.1979 (fr), *Kieft* 104 (BM, U, VEN); SE. of Páramo de Tamá, Pata de Judío, near the Colombia-Venezuela frontier, 2900–3000 m, 20.i.1968 (fl), *Steyermark & Dunsterville* 101230 (NY, VEN).

The following is a summary of the variation of *H. phellos* subsp. *phellos*. The variation is continuous, thus preventing the recognition of these variants as taxa. The names in single quotation marks are merely for reference and have no formal nomenclatural status.

Variant 3a (i) 'marcescens': Stems not differentiated, internodal corky emergences not pronounced; leaves eventually deciduous, drooping and marcescent, narrowly elliptic to oblanceolate, acute to acuminate, margin recurved (Santandér: Vetas, La Baja).

Variant 3a (ii) 'angustum': Stems not differentiated, internodal corky emergences evident; leaves eventually deciduous, drooping but not marcescent, oblanceolate to linear, acute, margin recurved (Norte de Santandér: Páramo de Fontibón, Mutíscua).

Variant 3a (iii) 'patens': Stems not differentiated, internodal corky emergences evident; leaves deciduous when spreading, oblanceolate to elliptic, acute to obtuse, margin recurved to plane (Santandér: Páramo de Santurbán, Norte de Santandér: Rio Chitagá, Táchira: Páramo de Batallón).

Variant 3a (iv) 'phellos': Stems not differentiated, internodal corky emergences evident; leaves deciduous after becoming ± appressed, narrowly elliptic to oblanceolate, acute, margin recurved to plane (Santandér: La Baja, Páramo de Romeral).

Variant 3a (v) 'diversicaule': Stems often differentiated, internodal corky emergences evident; leaves deciduous when spreading, broadly elliptic to obovate, acute to obtuse, margin recurved to plane (Norte de Santandér: Páramo de Fontibón, Mutíscua).

Variant 3a (vi) 'tamanum': Stems differentiated, internodal corky emergences evident; leaves deciduous when spreading or ascending, narrowly elliptic to oblong, subacuminate to acute, margin recurved (Norte de Santandér and Tachirá: Páramo de Tamá, Santandér: Páramo de Almorzadero).

The type specimen of *H. phellos* apparently belongs to variant 3a (iv) 'phellos'.

3b. **Hypericum phellos** subsp. **oroqueanum** N. Robson, **subsp. nov.**

a subsp. *phellos* foliis ad caulem continue adpressis differt. Type: Colombia, Cordillera Oriental, limites entre Los Departmentos Norte de Santandér y César, Jurisdicciones, Cerro de Oroque, 3000–3700–3900 m, 22–27.vii.1974, *Garcia Barriga & Jaramillo* 20629 (COL!, holotype).

Small tree 4 m tall, with shoots rounded, not differentiated; internodes with pronounced corky emergences. *Leaves* free, closely imbricate-appressed, tetrastichous, not or scarcely spreading, deciduous; lamina 5·5–8 × 1·6–2·2 mm, narrowly elliptic-oblong to oblanceolate, acute, margin plane. *Sepals c.* 7 × 2·5 mm, broadly elliptic. *Petals* 12–14 × 4–7 mm. *Stamens c.* 100. *Styles* 6–7 mm long.

Colombia (Norte de Santandér/César); 3700 m?
COLOMBIA. Known only from the type.

3c. **Hypericum phellos** subsp. **platyphyllum** (Gleason) N. Robson, **stat. nov.**

Hypericum platyphyllum Gleason in *Bull. Torrey bot. Club* **56**: 106 (1929) pro parte, excl. spec. *Killip & Smith* 15616. Type: Colombia, Norte de Santandér, Páramo de Romeral, 3800–4200 m, 30.i.1927 (fl), *Killip & Smith* 18626 (NY!, holotype; A!, COL, GH!, US!, isotypes).

Shrub 0·5–2 m tall, with shoots flattened terminally to rounded, not or slightly differentiated; internodes smooth. *Leaves* united by interfoliar ridge, ascending to closely imbricate, persistent; lamina 4–7 × 2–4 mm, broadly elliptic to obovate, obtuse to rounded, margin recurved to incurved. *Sepals* 5–7 × 2–3 mm, narrowly oblong to elliptic. *Petals* 8–14 × 4 mm. *Stamens c.* 80. *Styles* 5·5–7 mm long.

Colombia (Norte de Santandér, Santandér), confined to the Páramos de Santurbán and de Romeral; 2700–4100 m.

COLOMBIA. Norte de Santandér: Páramo de Santurbán, extremo este, 3300–3500 m, 27.vi.1940 (fl), *Cuatrecasas & Garcia-Barriga* 10297 (COL, F); Páramo de Romeral, hoya del río Cucutilla, 3600 m, 9.iv.1973 (veg), *Cuatrecasas & Jaramillo* 28751 (BM, COL, US). Santandér: Páramo de Santurbán, entre Berlin y Vetas, 3700–3800 m, 22.ix.1969 (fl), *Cuatrecasas & Rodriguez* 27897 (BM, COL, US); Páramo de Romeral, 3800–4100 m, 29–30.i.1927 (fl & fr), *Killip & Smith* 18580 (NY).

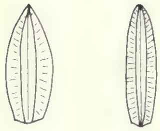
Killip & Smith 187716 (Páramo de Romeral) is intermediate between subsp. *platyphyllum* and subsp. *phellos*. Gleason (1929) confused subsp. *platyphyllum* with 29 *H. gleasonii* (q.v.).

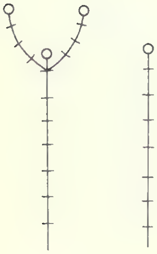
4. **Hypericum garciae** Pierce

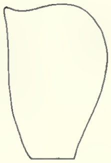
in *Bull. Torrey bot. Club* **70**: 174 (1943). Type: Colombia, Santandér, Páramo del Almorzadero, Peralonso, 3200–3300 m, 20.vii.1940 (fl), *Cuatrecasas & Garcia-Barriga* 9935 (F!, holotype; NY!, US!, isotypes).

Hypericum chamaemyrtus sensu Gleason in *Bull. Torrey bot. Club* **56**: 102 (1929), non Triana & Planchon (1862).

Hypericum ericifolium Steyerm. in *Fieldiana Bot.* **28**: 393 (1952) ['*ericaefolium*']. Type: Venezuela, Táchira, Páramo de Tamá, 2 km above Betania, 7 km above Villapaez, 2500 m, 14.vii.1944 (fl), *Steyermark* 57212 (F!, holotype; NY!, isotype).





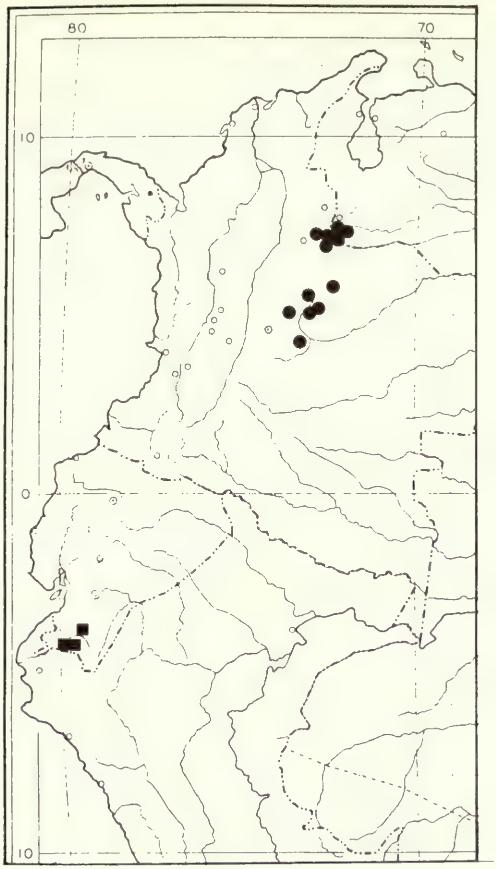


Shrub 0·3–1·2(–3) m tall, erect, with branches strict or ascending, lateral or occasionally pseudo-dichotomous. *Stems* orange-brown to blackish, 4-lined and ancipitous when young, the principal lines broader, eventually terete, without epidermal emergences, cortex exfoliating in strips; internodes 1–4 mm long. *Leaves* sessile, outcurving or ascending and subimbricate, tetrastichous, deciduous at suprabasal articulation; lamina 4–10 × 0·5–2·3 mm, elliptic-oblong or narrowly lanceolate to linear, broadly revolute and often concealing lower surface apart from midrib, not carinate, concolorous, lucent above, papillose beneath, not glaucous, coriaceous; apex acute, base cuneate, not sheathing, pairs united to form a narrow interfoliar ridge; basal vein unbranched; laminar glands dense, slightly prominent. *Inflorescence* 1(2)-flowered, terminal and on short lateral shoots, occasionally with pseudo-dichotomous branches; peduncle and pedicels 1·5–3 mm long, upwards incrassate; upper leaves foliose. *Flowers* 17–20 mm in diam., stellate. *Sepals* 4–9 × 1·7–3 mm, lanceolate to ovate, acute to subacuminate; veins 5–7, obscure, not visibly branching, midrib prominent; glands linear, distally punctiform. *Petals* bright to deep yellow, sometimes tinged red, 8–13 × 3–6·5 mm, 1·5–2 × sepals, narrowly obovate; apiculus acute; glands linear, interrupted distally. *Stamens* 40–70(?–100), longest 5–8 mm long, *c.* 0·6–0·65 × petals. *Ovary* 1·5–2·5 × 1–2 mm, ovoid; styles 3(4), 3·5–7 mm long, 2·2–2·5(–3) × ovary, free, spreading-incurved; stigmas small or slightly capitate. *Capsule* 4·5–5 × 3–3·5 mm, ovoid to subglobose, shorter than sepals. *Seeds c.* 1·3 mm long, ecarinate; testa finely scalariform.

In páramo, usually on dry stony or sandy soil; 2400–3935 m.

Colombia (Norte de Santandér to Meta), Venezuela (Táchira). Map 3.

COLOMBIA. Boyacá: Páramo de La Rusia, NW. to N. of Duitama, Serrania Peña Negra, Hoya de la Laguna Agua Clara, 3935 m, 10.xii.1972 (fl), *Cleef* 6992 (COL, U); Vado Hondo, Siberia, between Peña de Arnical and Alto de Mógotas, 3290 m, 4.iv.1973 (fr & fr), *Cleef* 9332 (BM, COL, U). Cundinamarca: Municipio de Tausa, páramo vecindad a la población, 3200 m, 26.x.1961 (fl), *Huertas & Camargo* 5285 (COL). Meta: Páramo de Sumapaz, Hoya El Nevado, Laguna El Sorbedero, 3550 m, 1.ii.1972 (fl), *Cleef* 1489A (COL). Norte de Santandér: Páramo de Hatico between Toledo and Pamplona, *c.* 2900 m, 12–13.iii.1927 (fl), *Killip & Smith* 20661 (K, NY, US). Santandér: Páramo del Almorzadero, 3600–3800 m, 28.xi.1941 (fl), *Cuatrecasas* 13496 (F, NY, P); Páramo Rico, near Vetas, 3750–3850 m, 18.i.1927 (fl), *Killip & Smith* 17659 (NY).



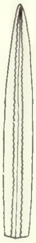
Map 3 4. *H. garciae* ●; 5. *H. acostanum* ■.

VENEZUELA. Táchira: Páramo de Tamá, El Paramito, 2550 m, viii.1939 (fl), *Chardon* 81 (VEN).

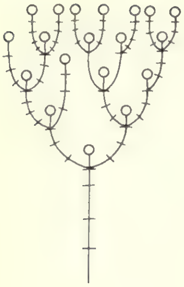
H. garciae differs from the coriacous-revolute-leaved form of *H. phellos* ssp. *phellos* ('patens') principally by its narrower, closely revolute leaves, a character that distinguishes it from all other species in sect. *Brathys*, except *H. acostanum* and *H. piriai*. In addition, these species are unique in having the leaf-base incorporated in the stem and forming a swelling, thus indicating that the leaf is not deciduous at the base. The largest flowers and leaves in *H. garciae* occur in Boyacá, whence there is a reduction trend along the Cordillera Oriental north-eastward to Táchira. As the variation is continuous, *H. ericifolium* cannot be recognized as a distinct species.

5. **Hypericum acostanum** Steyerm. [in Acosta-Solís, *Div. fitogeogr. y formac. geobot. Ecuador*: 103 (1968), nomen] ex N. Robson, **sp. nov.**

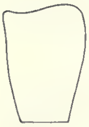
H. garciae Pierce affinis, sed foliis patulis persistentibus, pro ratione angustioribus, uninervis, margine revolutis, sepalis angustioribus, petalis longioribus, inter alia differt. Type: Ecuador, Loja, Cantón Catachocha, Hacienda La Hamaca, Loma Larga, 2200–2400 m, 15.iv.1944 (fl), *Acosta Solís* 7839 (F!, holotype; NY!, photograph).



Shrub 0·1–0·8 m tall, erect, with branches strict, pseudo-dichotomous and lateral. *Stems* orange-brown, 4-lined and ancipitous when young, the principal lines broader, eventually terete, without epidermal emergences, cortex exfoliating in strips; internodes 2–5 mm long. *Leaves* sessile, outcurving or spreading but not imbricate,



scarcely tetrastichous, persistent, not articulated but sometimes breaking off above base; lamina 8–22 × 0·5–2·5 mm, narrowly oblanceolate to linear, broadly to narrowly revolute, sometimes concealing lower surface apart from midrib, not carinate, paler or ferrugineous and smooth beneath, lucent above, not glaucous, coriaceous; apex acute, base parallel-sided, not sheathing, pairs united to form a narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense, impressed. *Inflorescence* 1-flowered, terminal, often with pseudo-dichotomous branches; pedicel 3–15 mm long, not upwards incrassate; upper leaves foliose. *Flowers* 20–25 mm in diam., stellate. *Sepals* 6–9 × 1–1·5 mm, narrowly triangular-lanceolate to oblong-linear, acute, sometimes revolute above; veins 5–7, obscure, not visibly branching, midrib slightly prominent; glands linear, distally punctiform. *Petals* bright (?) yellow, tinged red in bud, 10–14 × 5–7 mm, *c.* 2 × sepals, obovate; glands linear and striiform. *Stamens c.* 100, longest 4–5 mm long, *c.* 0·4 × petals. *Ovary c.* 2 × 1 mm, narrowly ovoid; styles 3, 3–3·5 mm long, *c.* 1·5 × ovary, divergent; stigmas broadly capitate. *Capsule* 4–5 × 3–4 mm, ovoid-subglobose, shorter than sepals. *Seeds c.* 1 mm long, ecarinate; testa finely scalariform.



On steep shrubby slopes of páramo; 2200–3300 m.

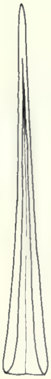
Ecuador (Loja, Morona-Santiago). Map 3.

ECUADOR. Loja: between San Pedro and Portovelo, slope towards Portovelo, *c.* 2300 m, 13.x.1955 (fl & fr), *Asplund* 18133 (S); Celica-Guachanamá road, Km 8 at the Roldós memorial monument, 2700 m, 19.ii.1985 (fl & fr), *Harling & Anderson* 2223 (BM, GB).

H. acostanum is clearly related to *H. garciae*, for which the nearest record is from central Colombia (Meta).

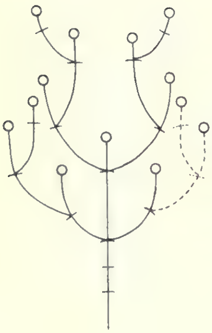
6. **Hypericum piriai** Arechav.

in *An. Mus. nac. Montevideo* **3**: 108 (1898), *Fl. Uruguay* **1**: 108 (1898); L. B. Sm. in *J. Wash. Acad. Sci.* **48**: 314 (1958); Rodríguez Jiménez in Reitz, *Fl. Ill. Catarin., Hipericáceas*: 5, fig. 1 B (1980). Type: Uruguay, Mardonado, Pan de Azúcar cerca del Castillo de Piriápolis, xi.189– (fl & fr), *Arechavaleta* (MVM, holotype; GH!, US!, photographs).



H. tenuifolium St.-Hil. in St.-Hil., Jussieu & Cambess., *Fl. Bras. Merid.* **1**: 337 (1828); Walpers, *Repert. Spec. nov.* **1**: 390 (1842); Dietrich, *Syn. Pl.*: 1236 (1847); Reichardt in Martius, *Fl. Brasil.* **12**: 188 (1878), non Pursh (1814). Type: Brazil, Sao Paulo, prope urbes Sancti Pauli, Villa do Castro et Curityba, iii.1820 (fl & fr), *St.-Hilaire* 1174 (P!, holotype; US!, photograph).

H. hilaireanum L.B. Sm. in *J. Wash. Acad. Sci.* **48**: 314 (1958); Angely, *Fl. Anal. Paraná*: 451 (1965). Type as for *H. tenuifolium* St.-Hil.



Subshrub or perennial herb 0·07–0·35 m tall, erect, with taproot, branches few, strict or decumbent, lateral, from base or lower half of stem. *Stems* green, 4-lined above, eventually terete, gland-dotted, with ± prominent glands along raised lines; cortex eventually exfoliating in strips; internodes 3–21 mm long. *Leaves* sessile, outcurving and deflexing, not tetrastichous, persistent, not articulated but occasionally breaking off above base; lamina 10–40 × 1–2 mm, linear, revolute, concealing all or most of lower surface apart from midrib, not carinate, paler beneath?, dull above, ± glaucous, subcoriaceous; apex acute to acicular, base parallel, not sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense, slightly impressed or not. *Inflorescence* 1–18(–25)-flowered, terminal and sometimes axillary, monochasial after first branching; pedicels 3–6 mm long; upper leaves bracteose. *Flowers* 8–20 mm in diam., obconic to pseudotubular. *Sepals* 6–16 × 1·5–2·5 mm, linear-lanceolate to lanceolate or narrowly oblong, acute to acuminate, margin slightly revolute or plane; veins 3–5, unbranched, midrib slightly prominent or not; glands linear towards base or wholly punctiform. *Petals* bright (?) yellow, not (?) tinged red in bud, 7–12 × 3–4·5 mm, 0·8–1·2 × sepals, obovate-oblong; glands linear, distally punctiform. *Stamens* 25–60, longest 5–8(–10) mm, *c.* 0·75 × petals, 3(5)-fascicled, the double (antesepalous) fascicles sometimes incom-

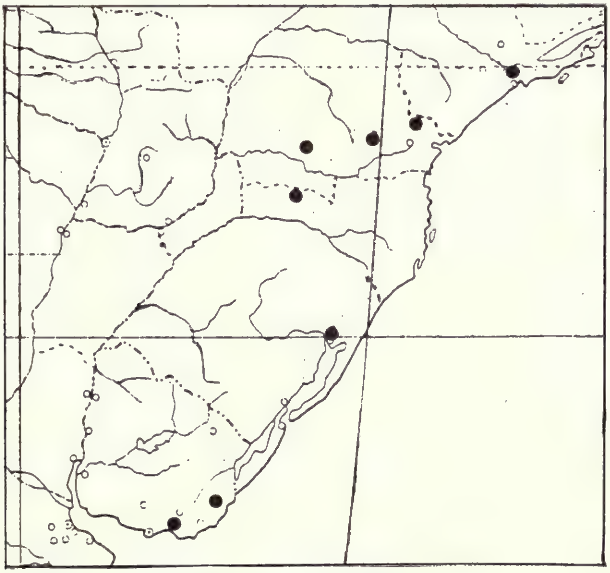
pletely united, with filaments within each fascicle united shortly or usually to 0·7 of their length. *Ovary* 1·5–4 × 1–1·5 mm, narrowly ovoid to narrowly ovoid-ellipsoid; styles 3, 2–4 mm long, *c.* 1–1·3 × ovary, outcurving; stigmas subcapitate. *Capsule* 5–7 × 2·2–3 mm, ovoid-cylindric to ellipsoid, shorter than sepals. *Seeds* 0·8–1 mm long, ecarinate; testa finely scalariform.

In dry, stony or damp grassland; lowland to 1000 m.

Brazil (São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Uruguay. Map 4.

BRAZIL. São Paulo: São Paulo to Villa Emma, xii.1933 (fl), *Brade* 12978 (MO). Paraná: Municipio Guarapuava, estrada para Laranjeiras do Sul, 15.xi.1957 (fl), *Hatschbach* 4253 (US); Municipio Ponta Grossa, Parque Vila Velha, Furnas, i.x.1965 (fl & fr), *Hatschbach* 12854 (K). Santa Catarina: Municipio Abelardo Luz, 8–12 km N. of Abelardo Luz, 900–1000 m, 15.xi.1964, *Smith & Klein* 13305 (NY, US); Municipio Xanxere, 11 km N. of Abelardo Luz, 500–600 m, 25.xii.1956, *Smith & Klein* 9231 (US). Rio Grande do Sul: Vila Manresa, prope Porto Alegre, 21.x.1951, *Rambo* 51325 (US); Porto Alegre, Morro da Policias, 21.ii.1902 (fl & fr), *Malme* Regn. II 1408 (S).

URUGUAY. Mardonado: see type. Lavalleja: Co. Penitente, 10.i.1909 (fl), *Berro* 5533 (US).



Map 4 6. *H. piriai* ●.

Despite the considerable distance between southern Ecuador and south-eastern Brazil, there can be no doubt that *H. piriai* is a close relative of *H. acostanum*. The character trends between *H. garciae* and *H. acostanum* are extended to *H. piriai* (for example: tall tall shrub–dwarf shrub–subshrub to herb; leaves short, deciduous –long, persistent; sepals short, broad–long, narrow, revolute–long to short, narrow, revolute to plane). However, the flower shows new tendencies, viz. (i) towards development of a cymose inflorescence and (ii) to become adapted to specialized rather than open pollination. Unlike the other examples of this change in *Hypericum* (*H. elodes* and the species of sect. 25. *Adenotrias*), *H. piriai* shows intermediate evolutionary stages and the specialization is less complex. Thus (i) the flower apparently varies from obconic to pseudotubular and the stamen filaments within each fascicle vary correspondingly from almost free to *c.* 0·7 united; (ii) the double fascicles are often incompletely united; (iii) there are no fasciclodes to help open the flower by expansion and no ligules on the petals to guide the tongues of foraging insects.

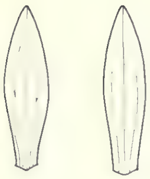
I agree with Rodríguez Jiménez (1980) that *H. piriai* cannot be divided into a northern species (*H. hilaireanum*) and a southern one (*H. piriai* sensu stricto). The more northern ones, suffruticose with fewer larger flowers and longer sepals, are the nearest morphologically to *H. acostanum*.

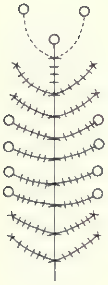
7. **Hypericum irazuense** Kuntze [*Rev. Gen. Pl*: 61 (1891), in synon.; Williams in *Fieldiana Bot.* **29**: 355 (1961), nomen] ex N. Robson, **sp. nov.**

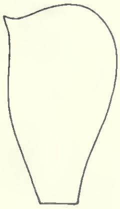
H. phellos subsp. *oroqueano* N. Robson affinis, sed foliis persistentibus nervis haud ramosis, differt; a *H. stenopetalo* Turcz. foliorum nervis basalibus haud ramosis floribus maioribus, stylis longioribus, differt. Type: Costa Rica, Cartago, Volcán Irazú, 3150 m, 25.vi.1874 (fl), *Kuntze* 2359 (NY!, holotype; K!, isotype).

H. caracasanum var. *scherzeri* J. Zahlbr., in sched.
H. silenoides sensu R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* **3**(6): 214 (1893), in *Bull. Herb. Boissier* **6**: 258 (1898), in *op. cit.* II, **8**: 177 (1908), in *Engler & Prantl, op. cit.,* 2nd ed. **21**: 181 (1925), non Juss. (1804).

Icon: Fig. 5A.







Shrub or small tree 0·4–5 m tall, erect, flat-topped, with branches strict, lateral and sometimes pseudo-dichotomous, *Stems* yellow-brown, 4-lined and ancipitous when young, becoming terete, with transverse corky emergences, cortex exfoliating in strips; internodes 1·5–4 mm long. *Leaves* sessile, imbricate and tetrastichous at first, spreading then becoming appressed, tardily deciduous near the base (usually after withering) or persistent; lamina 10–15 × 1·5–3·5 mm, narrowly elliptic to oblanceolate, plane to recurved, not carinate, concolorous, not glaucous, subcoriaceous to coriaceous; apex acute, base cuneate, not sheathing, pair free but with incomplete narrow interfoliar ridge; basal veins 3–5, parallel, inner pair (of 5) branching above, tertiary reticulation not visible; laminar glands rather dense, impressed above, not prominent beneath. *Inflorescence* 1-flowered, terminal and on short lateral shoots, with extension shoots from 2–3 nodes below; pedicel 2·5–4 mm long; upper leaves bracteose. *Flowers* 25–30 mm in diam., stellate. *Sepals* 7·5–9 × 1·5–2 mm, linear-lanceolate, acute; veins 5, unbranched, midrib not prominent; glands mostly linear, punctiform near apex. *Petals* bright yellow to orange-yellow, not (?) tinged red, 13–18 × 7–10 mm, *c.* 2 × sepals, oblanceolate to obovate; apiculus acute; glands linear, interrupted distally. *Stamens c.* 100, longest 6–9 mm long, 0·35–0·5 × petals. *Ovary* 1·5–2·5 × 1–1·5 mm, ovoid; styles 3, 9–10 long, 4–6 × ovary, free, spreading, distally incurved; stigmas small. *Capsule* 6–7 × 4–5 mm, broadly ovoid or ellipsoid to globose, shorter than sepals. *Seeds* 1–1·3 mm long, scarcely carinate; testa finely scalariform. 2n = 12.

On open páramo slopes or among bamboo (*Chusquea*); 2700–3730 m.

Costa Rica (San José, Cartago, Limón), on the cordillera and on Volcán Irazú and V. Turrialba, and in adjacent Panama (Chiriquí). Map 5 (p. 32).

COSTA RICA. Cartago: Volcán Irazú, 3000–3300 m, 5.v.1928 (fl), *Stork* 2011 (F, MICH, NY); Finca Quemado to top of Volcán Turrialba, 2800–3200 m, 10.v.1971 (fl), *Wilbur* 14319 (DUKE); Cordillera de Talamanca, Cerro de la Muerte, Pan-American Hwy., 5 km above Millsville, 3400–3500 m, 22.vii.1949 (fl), *Holm & Iltis* 458 (F, K, NY, P). Limón: Chirripó National Park, between Casa de Administración and peak, *c.* 3400 m, 13.ii.1983 (fl & fr), *Garwood et al.* 1161 (BM). San José: Upper Río Talari, lower Valle de los Conejos and trail to Valle de los Leones, 3250–3450 m, 21–23.viii.1971 (fl & fr), *Burger & Gomez P.* 82848 (BM, DUKE, F); La Asunción, Cerro Sákira, 3400 m, 27.i.1968 (fl), *Wilbur & Stone* 10047 (DUKE, F, MO).

PANAMA. Chiriquí: Cerro Fabrega and vicinity near Costa Rican frontier, 3150–3335 m, 7–8.iv.1976 (fl), *Weston* 10189 (MO).

H. irazuense has apparently been derived from *H. phellos* subsp. *oroqueanum* in a similar way to the derivation of *H. stenopetalum* from *H. phellos* subsp. *phellos*, but it can be distinguished from *H. stenopetalum* both morphologically and geographically.

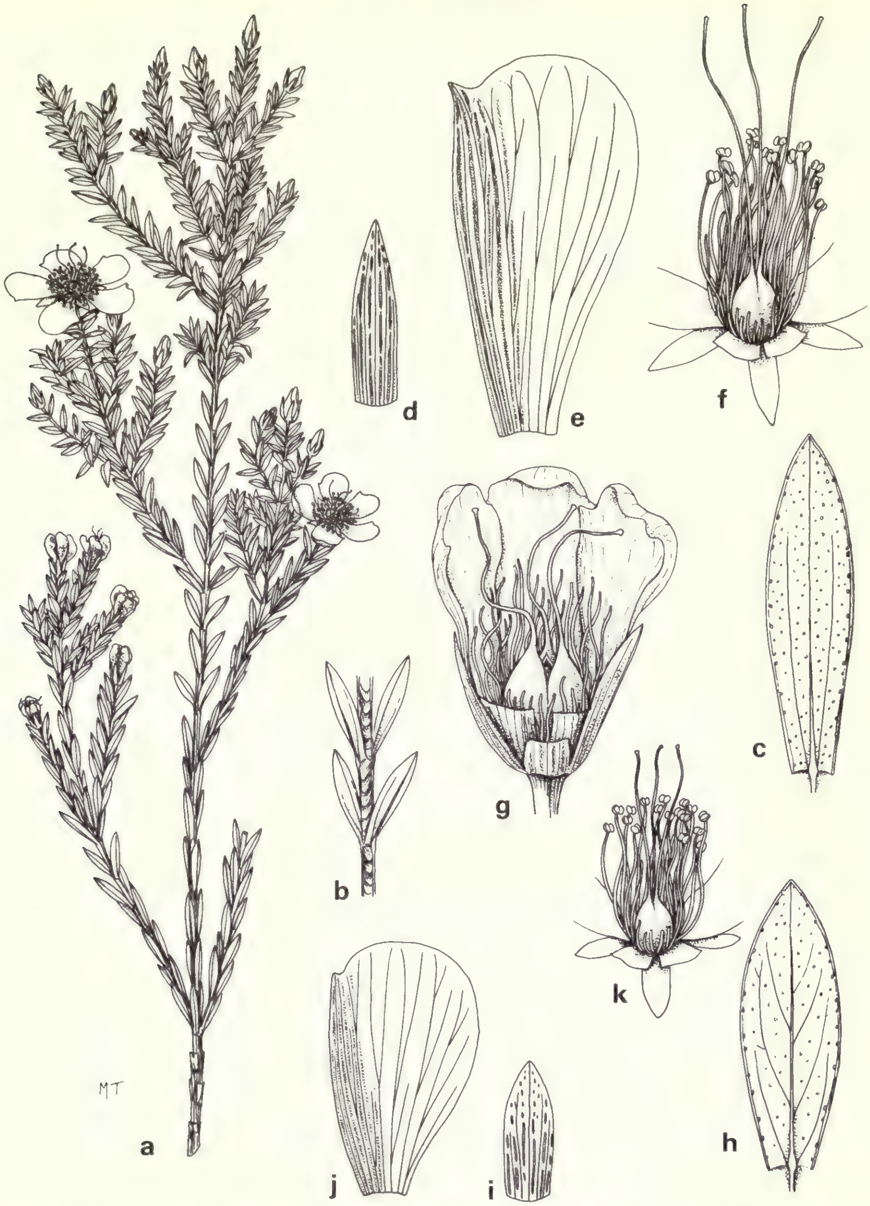
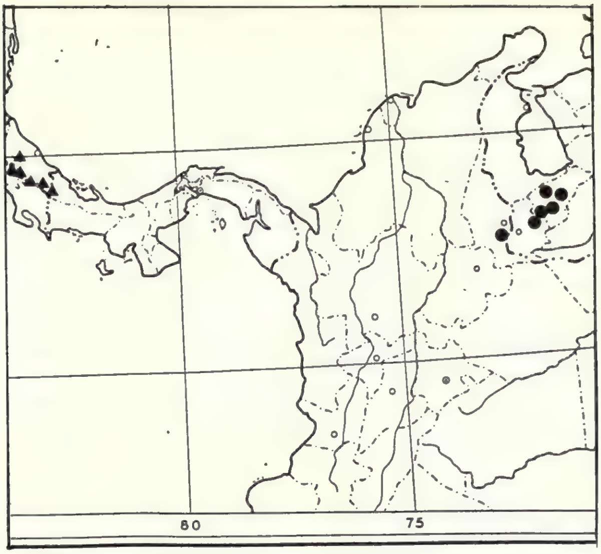


Fig. 5 A. *H. irazuense*: (a) habit; (b) stem with leaves; (c) leaf; (d) sepal; (e) petal; (f) stamens (partly cut away) and ovary; (g) capsule. B. *H. stenopetalum*: (h) leaf; (i) sepal; (j) petal; (k) stamens (partly cut away) and ovary (a × ½; b × 1; d–g, i–k × 3; c, h × 4). A. *Khan, Vickery & Tebbs* 1398; B. *Luteyn* 6032.

The record of *H. irazuense* from Guatemala is apparently erroneous. A Guatemalan label was used for the Kew (K) specimen of *Friedrichstal* 1395, but the Chicago (F) specimen of this collection has a similar label with 'Guatemala' crossed out and replaced by 'Cartago'.

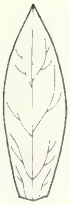
8. **Hypericum stenopetalum** Turcz.

in *Bull. Soc. Nat. Moscou* **31** (1): 385 (1858). Knuth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 484 (1927); Gleason in *Bull. Torrey Bot. Club* **56**: 103 (1929). Type:



Map 5 7. *H. irazuense* ▲; 8. *H. stenopetalum* ●.

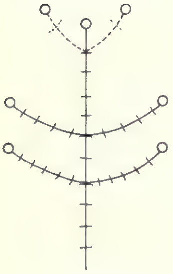
Venezuela, Mérida, Sierra Nevada, 2940 m, 1846 (fl), *Funck & Schlim* 1139 (LE, holotype; BM!, P!, isotypes).

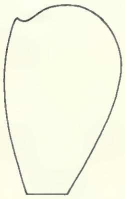


H. decorticans Planchon & Linden in Weddell, *Chloris Andina* **2**: 272 (1861); Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 297 (1862), nomen.

H. meridense Steyerm. in *Fieldiana Bot.* **28** (2): 394. (1952). Type: Venezuela, Mérida, between San José and Beguilla, Páramo de Pozo Negro, 2590–3220 m, 3.v.1944 (fl & fr), *Steyermark* 56272 (NY!, holotype; F!, isotype).

Icon: Fig. 5B.





Shrub or small tree 0·5–4 m tall, erect, branches strict or ascending, lateral or rarely pseudo-dichotomous. *Stems* yellow-brown, 4-lined and ± ancipitous when young, becoming terete, without or with weak corky emergences, cortex exfoliating in strips; internodes 1·5–3 mm long. *Leaves* sessile, imbricate and tetrastichous at first, becoming appressed, eventually deciduous near base or persistent; lamina 4–15 × (1–)1·5–4·5 mm, narrowly or rather broadly elliptic to oblanceolate, plane or recurved or rarely concave to cucullate, not or scarcely carinate, concolorous, not glaucous, subcoriaceous to coriaceous; apex shortly acuminate to subacute, base cuneate to angustate, not sheathing, pairs free but with incomplete narrow interfoliar ridge; basal veins 3–5, diverging, all or only midrib branching, tertiary reticulation obscure or not visible; lamina glands rather dense, impressed above, ± prominent beneath. *Inflorescence* 1-flowered, terminal and sometimes on ± short lateral shoots, with extension shoots usually from 2nd or 3rd node below; pedicel 1–9 mm long; upper leaves foliose or bracteose. *Flowers* 15–27 mm in diam., stellate. *Sepals* 4–9 × 1·5–3 mm, narrowly oblong or elliptic to ovate-lanceolate or rarely oblanceolate, acute or shortly acuminate to obtuse; veins 5–7, branched distally or not, midrib not or scarcely prominent; glands mostly linear or up to half punctiform. *Petals* bright yellow to orange-yellow, sometimes margined red, (6–)8–15 × 4–8 mm, *c.* 2 × sepals, oblanceolate to obovate; apiculus acute; glands all linear or distally interrupted. *Stamens* 65–120, longest 5–8 mm long, 0·5–0·7 × petals. *Ovary* 2–3 × 1–2 mm, ± broadly ovoid; styles 3, (5–)6–9 mm long, 2–4 × ovary, free, spreading, distally incurved; stigmas small or subcapitate. *Capsule* 4–6 × 3·5–5 mm, broadly ovoid to globose, shorter than sepals. *Seeds c.* 1 mm long, ecarinate; testa finely scalariform.

On open scrubby or stony páramo slopes and among shrubs or bamboos in the tree/shrub zone immediately below them; 2580–4200 m.

Colombia (Santandér), Venezuela (Táchira, Mérida). Map 5.

COLOMBIA. Santandér: [Páramo de Almorzadero] Peralonso, Timocato, 3600 m, 29.ix.1969 (fl), *Cuatrecasas & Rodriguez* 27871 (BM, COL, US); Páramo de Santurbán, *c.* 3000 m, 27.viii.1948 (fl), *Barkley & Araque M.* 18s169 (COL, US).

VENEZUELA. Mérida: Páramo de Los Leones (La Lagunita, La Cañada Grande) al W. de Murucubá, 3400–3500 m, 31.v.1930 (fl), *Gehringer* 159 (F, NY, VEN); Páramo de San José, monte El Cupío, 3000 m, 1.ii.1973 (fl & fr), *Cuatrecasas, Ruiz-Teran & López-Figueras* 28440 (BM, US). Táchira: Páramo de Portachuelo, 2860 m, 23.x.1978 (fl), *Luteyn* 6032 (BM, MO, NY, VEN).

Linden 446 (BM, K, W) is labelled 'Caracas'. In the absence of other records from that area this probably merely indicates Venezuela.

9. **Hypericum carinosum** R. Keller

in *Bull. Herb. Boissier,* II, **8**: 182 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Knuth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 483 (1927); Gleason in *Bull. Torrey bot. Club* **56**: 102–103 (1929). Type: Venezuela, Mérida, Páramo de Portachuelo, 2600–2700 m, 1846 (fl), *Funck & Schlim* 1459 (W!, holotype; BM!, P!, isotypes).

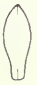
H. nova species sensu Turcz. in *Bull. Soc. Nat. Moscou* **31** (2): 386 (1858); Knuth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 484 (1927).

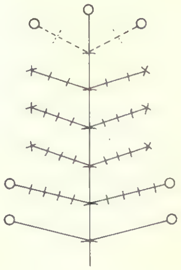
H. struthiolifolium sensu Trev., *Hyper. Animad*: 15 (1861) ['*struthiolaefolium*'] pro parte, excl. typum.

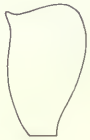
H. thymifolium sensu Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 297 (1862) pro parte, quoad syn. Trevirani.

H. stenoclados Cuatrec. in *Ciencia Mex.* **4**: 64 (1943). Type: Colombia. Santandér, Páramo de Almorzadero, extremo sur, Peralonso, 3200 m, 19.vii.1940 (fl), *Cuatrecasas & Garcia Barriga* 9919 (COL, holotype; F!, NY!, US! isotypes).

Shrub 0·6–*c.*2·5 m tall, erect, with branches strict, lateral, short (flowering) and long (extension). *Stems* purplish-brown, 4-lined and ancipitous when young, eventually terete, without epidermal emergences, cortex exfoliating in strips; internodes 2–9 mm long. *Leaves* sessile, spreading from the base or ascending but not imbricate or tetrastichous, persistent; lamina 3·5–5 × 0·8–2 mm, narrowly elliptic or narrowly oblong to oblanceolate-spathulate, plane, rarely apically subconcave, markedly carinate, concolorous, not or slightly glaucous, chartaceous to subcoriaceous; apex acute to subacute, base cuneate to angustate, not sheathing, pairs almost free (interfoliar ridge rudimentary); basal vein 1, unbranched; laminar glands dense, not impressed above, prominent beneath. *Infloresence* 1–2(–3)-flowered, terminal and on short lateral pinnate branches; peduncle and pedicels *c.* 2 mm long; upper leaves bracteose. *Flowers* 8–13 mm in diam., stellate. *Sepals* 2–4·5 × 0·5–1·8 mm, ovate-lanceolate to triangular-lanceolate, acute; veins 3(5), unbranched, midrib distally incrassate; glands linear, interrupted distally. *Petals* bright (?) yellow, 4–8 × 2–3 mm, *c.* 2 × sepals, oblong-lanceolate to obovate; apiculus acute; glands linear, interrupted distally. *Stamens* 40–80, longest 3–4 mm long, 0·5–0·6 × petals. *Ovary* 1·5–2 × 0·8–1 mm, ovoid; styles 3, 4–6(–7) mm long, *c.* 2–3 × ovary; stigmas small. *Capsule c.* 4 × 3·5 mm, subglobose, shorter than sepals. *Seeds* not seen.







In thickets and woodland margins in the páramo; 2600–3200 (–4500) m.

Colombia (Norte de Santandér, Santandér), Venezuela (Mérida). Map 6 (p. 37).

COLOMBIA. Norte de Santandér: environs of Pamplona. 10.x.1943 (fl), *de Garganta* 626 (F). Santandér: vicinity of Las Vegas, 2600–3600 m, 21–23.xii.1926, *Killip & Smith* 15921 (GH, NY, US); vicinity of California, 2800 m, 11–27.i.1927, *Killip & Smith* 16904 (F, GH, NY, US).

VENEZUELA. Mérida: Páramo de Los Leones, 3400–4500 m, 31.v.1930 (st), *Gehringer* 149 (VEN).

H. carinosum is related to *H. phellos* subsp. *phellos* 'diversicaule', and its area of distribution is to the south-east of that of the latter. The two taxa, however, are quite distinct, *H. carinosum* being recognizable (inter alia) by the stem internodes without corky emergences, the smaller, persistent, 1-nerved leaves, and the smaller flowers.

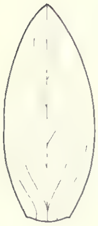
H. stenoclados has subacute, subcoriaceous leaves rather than the acute, chartaceous leaves typical of *H. carinosum*, but these differences do not merit taxonomic recognition.

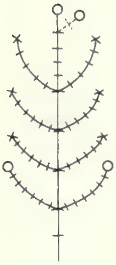
10. **Hypericum simonsii** N. Robson, **sp. nov.**

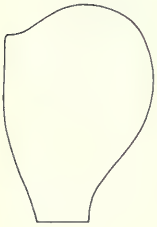
H. phellos affinis, sed caulis haud suberosis, foliis persistentibus deflexis oblongis apice rotundatis basi conjunctis venatione valde reticulata, sepalis subacutis vel rotundatis, stylis (5–)6–9 mm longis, differt. Type: Colombia, Magdalena, Sierra Nevada de Santa Marta, 1880 (fl), *Simons* s.n. (BM!, holotype).

H. stenopetalum [var.] β *majus* Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 297 (1862) ['major']. Types: Colombia, Magdalena, Santa Marta, source ['prov.'] of Rio Hacha, 3700–3800 m, vii.1844 (fl & fr), *Purdie* s.n. (G, lectotype; GH!, K!, syntypes); ibid., 1851–1852 (fl), *Schlim* 838 (G, syntype).

Icon: Fig. 6A.







Shrub 1–2 m tall, erect, with branches ascending, mostly lateral. *Stems* reddish-brown, 4-lined when young, eventually terete, without epidermal wrinkles, cortex flaking irregularly; internodes 2–10 mm long. *Leaves* sessile, spreading from the base, not tetrastichous, becoming brown and deflexed, usually persistent until cortex is shed; lamina (7–)8–16(–20) × (2·2–)3–5·2(–7) mm, narrowly elliptic to narrowly oblong, plane, not concave or carinate, concolorous, pale green, chartaceous; apex rounded, base cuneate, not sheathing, pairs united to form a narrow interfoliar ridge; basal or near-basal veins 5–7, with branches and tertiary reticulation rather conspicuous; laminar glands dense, visible beneath only. *Inflorescence* 1 (2)-flowered, mostly terminal and lateral, occasionally pseudo-dichotomous; peduncle and pedicels 4–7 mm long; upper leaves not transitional. *Flowers* 20–35 mm in diam., stellate. *Sepals* 6–10·5 × 2·4–3·5 mm, lanceolate or narrowly elliptic to narrowly oblong or oblanceolate, subacute to rounded; veins 5–7, not or obscurely branched, midrib not prominent; glands distally punctiform. *Petals* bright yellow, 10–21 × 7–13 mm, *c.* 2 × sepals, oblanceolate; apiculus obtuse; glands distally interrupted. *Stamens c.* 100, 'obscurely 5-fascicled', longest *c.* 7 mm long, 0·4–0·5 × petals. *Ovary* 2·5–3·5 × 2·5 mm, ovoid; styles 3–4, 4·5–6 mm long, *c.* 2 × ovary, spreading, distally incurved; stigmas narrowly capitate. *Capsule c.* 8 × 5 mm, subglobose, shorter than sepals. *Seeds* not seen.

In páramo, bushy prairies, and thickets; 3250–4100 m.

Apparently confined to the Sierra Nevada de Santa Marta in Colombia (Magdalena). Map 2 (p. 24).

COLOMBIA. Magdalena: near Río Seville, 20.i.1959 (fl), *Barclay & Juajibioy* 6557 (MO, NY); Sierra de Santa Marta, *c.* 48 km inland from Dibulla, *c.* 3850 m, vii.1932 (fl), *Seifriz* 455 (US); Sierra de Santa Marta, SE. slopes, Hoya del Río Donachuí, Meollaca, 3320–3260 m, 29.ix.1959, *Cuatrecasas & Romero-Castañeda* 24480 (COL, US); Sierra de Santa Marta, source of Río Donachuí, 4310 m, 22.v.1977, *Starker White & Alverson* 547A (NY); Sierra de Santa Marta, quebrada from Laguna Río Frío, 3250 m, 28.vii.1972, *Kirkbride & Forero* 1751 (BM, COL).

H. simonsii, which is apparently confined to the Sierra de Santa Marta massif, is related to *H. phellos* (Venezuela-Colombia border area). It is morphologically more specialized in that its leaves are united by an interfoliar ridge, but it is more primitive in that they have 5–7 basal or near-basal veins.

11. **Hypericum papillosum** N. Robson, **sp. nov.**

H. simonsii N. Robson affinis, sed habitu humiliore densiore, foliis sepalisque subtiliter papillosis, foliis angustioribus apice obtusis vel rotundatis basi breviter vaginatis, stigmatibus valde capitatis, differt. Type: Colombia, Boyacá, Sierra

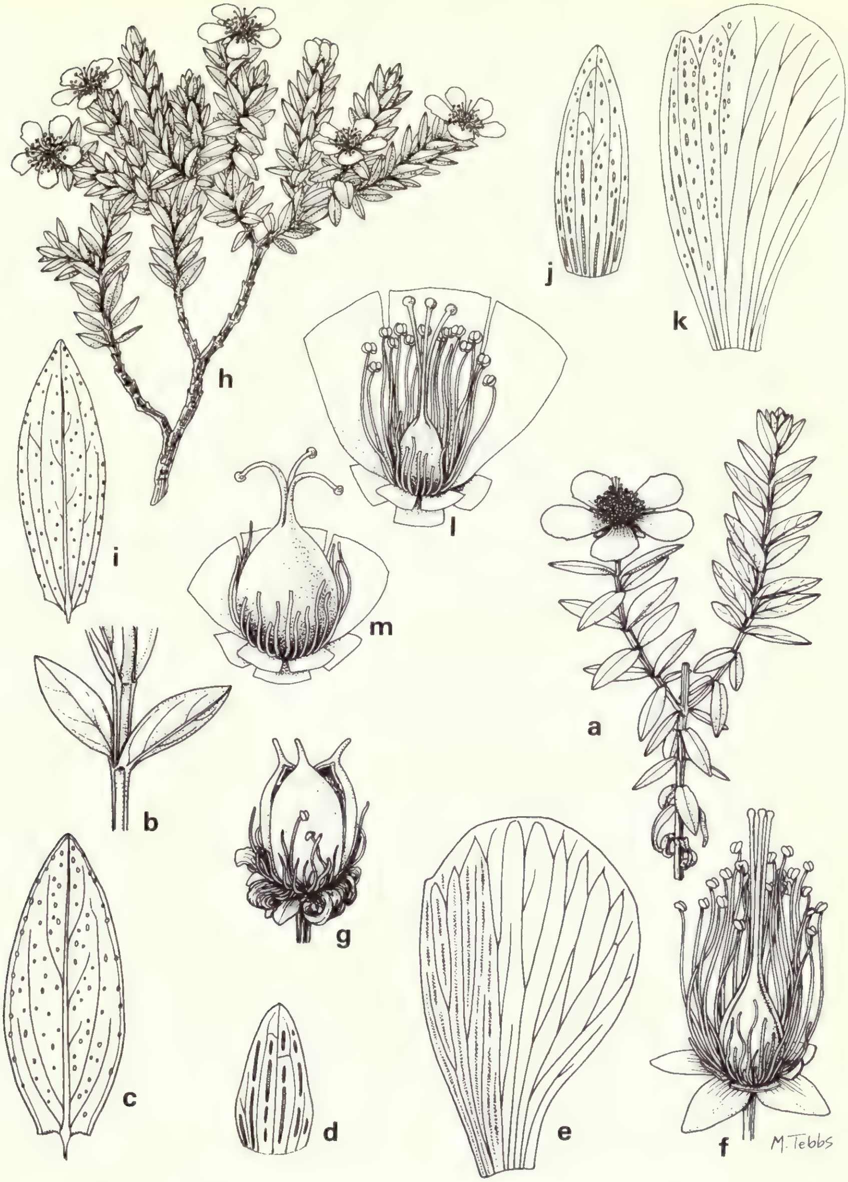
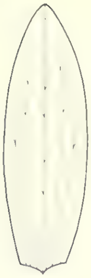


Fig. 6 A. *H. simonsii*: (a) habit; (b) stem with leaves; (c) leaf; (d) sepal; (e) petal; (f) stamens (partly cut away) and ovary; (g) capsule. B. *H. papillosum*: (h) habit; (i) leaf; (j) sepal; (k) petal; (l) stamens (partly cut away) and ovary; (m) young capsule (a, h × ½; b × 1; c–f × 4; g × 2; i–m × 3). A. *Romero-Castañeda* 4541; B: (h) *Grubb, Curry & Fernandez-Perez* 401; (i–m) *Jaramillo Mejía* 2728A.

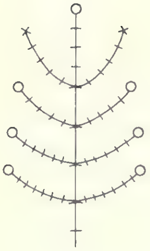
Nevada del Cocuy, above Laguna Grande, *c.* 3900 m, 14.viii.1957 (fl), *Grubb, Curry & Fernandez-Perez* 401 (K!, holotype; US!, isotype).

Icon: Fig. 6B.

Shrub to *c.* 1 m tall, erect, rounded, with branches ascending or spreading, mostly lateral. *Stems* orange-brown, 4-lined and ancipitous when young, eventually terete, without epidermal wrinkles, cortex flaking irregularly; internodes 2–9 mm long. *Leaves* sessile, spreading from base or just above base, not tetrastichous, becoming brown and deflexed, persistent until cortex is shed; lamina 10–22 × 4–7 mm,



narrowly elliptic to narrowly oblong, plane, not concave or carinate, finely papillose on both sides, concolorous, pale green, chartaceous; apex obtuse to rounded, base cuneate, shortly sheathing at least when young, pairs united to form narrow interfoliar ridge; basal or near-basal veins 3–7, with branches and tertiary reticulation inconspicuous; laminar glands rather dense, visible on both sides or only beneath. *Inflorescence* 1-flowered, mostly terminal and lateral, occasionally pseudo-dichotomous; pedicel 4–6 mm long; upper leaves not transitional. *Flowers c.* 30 mm in diam., stellate. *Sepals* 9–11 × 3–5 mm, oblong to lanceolate-oblong or oblanceolate, subacute to obtuse, with epidermis papillose; veins 5, laterals branched, midrib prominent; glands mostly punctiform. *Petals* bright yellow, 14–17 × 9–10 mm, *c.* 1·5–1·8 × sepals, oblanceolate; apiculus obtuse; glands striiform or punctiform. *Stamens c.* 100, *c.* 7 mm long, longest *c.* 0·5 × petals. *Ovary c.* 2·5 × 2 mm, ovoid; styles 3, *c.* 5 mm long, *c.* 2 × ovary, spreading, distally incurved; stigmas distinctly capitate. *Capsule* and *seeds* not seen.

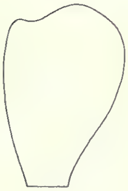


On dry rocky slopes in páramo and subpáramo; 3530–*c.*3900 m.

Colombia (Boyacá). Apparently confined to the Sierra Nevada del Cocuy and the Páramo de Pisva/Páramo de Chitá. Map 2 (p. 24).

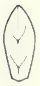
COLOMBIA. Boyacá: Páramo de Pisva, road between Socha and La Punta, Km 61, 5·5 km E. of Los Pinos, 3680 m, 14.vi.1972 (fl), *Cleef* 4541 (U); same road, Km 70, 1·5 km, W. of El Cadillal, 3530 m, 16.vi.1972 (fl), *Cleef* 4631 (U); Páramo de Chitá, vertiente oriental, sitio Piedras Negras, 3500–3700 m, 13.vii.1967 (fl), *Jaramillo & van der Hammen* 2728A (COL).

The papillose leaf- and sepal-epidermis (making them appear duller green) clearly distinguish this isolated endemic of Dept. Boyacá from *H. simonsii* and, indeed, from nearly all other species in sect. *Brathys*. It also differs from *H. simonsii* in the obscure or almost invisible tertiary leaf-venation.



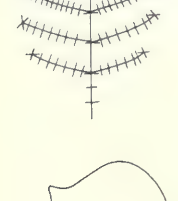
12. **Hypericum lycopodioides** Triana & Planchon

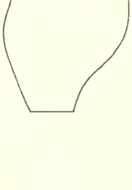
in *Annls Sci. nat.* (Bot.) IV, **18**: 296 (1962). Type: Colombia, Cundinamarca, Andes de Bogotá, Cipaquira [Zipaquirá], viii.1855, (fl), *Triana* 5464 (COL?, holotype; BM!).



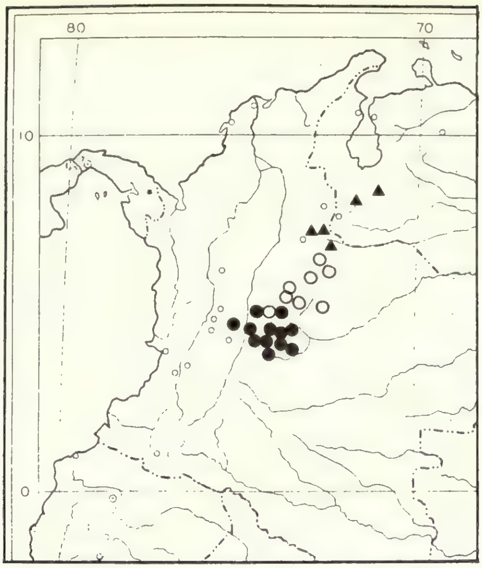
H. gyropodioides sensu Jackson & Hooker, *Index Kew.* **1**: 1193 (1893), sphalm.

Shrub 0·8–2·5 m tall, erect, with branches strict to ascending, lateral, short (flowering) and long, narrowly spiciform to cylindric (extension). *Stems* dark red-brown, 4-lined when young, eventually terete, without epidermal emergences, cortex exfoliating in strips or small flakes; internodes 1·5–2·5 mm long. *Leaves* sessile, imbricate to spreading, eventually reflexed, markedly terastichous; lamina 3–6 × 1·5–3 mm, oblong to elliptic or lanceolate, incurved-conduplicate, midrib usually prominent beneath, margin narrowly hyaline and plane or undulate, not glaucous, subcoriaceous; apex acute to acuminate, slightly cucullate, base broadly cuneate to angustate, loosely clasping, pairs united to form narrow interfoliar ridge; basal vein 1, sometimes branched; laminar glands dense, not impressed or prominent, visible on both sides. *Inflorescence* 1-flowered, terminal and on short lateral branches; pedicels absent; upper leaves foliose, appressed to calyx. *Flowers* (15–)25–30 mm in diam., stellate. *Sepals* (5–)6–7 × (2–)2·5–3 mm, ovate-oblong to ovate-lanceolate, acute to obtuse, ± subcucullate, margin hyaline; veins 7, unbranched, midrib scarcely prominent; glands linear, interrupted distally. *Petals* bright yellow, 13–16 × 9–10 mm, 2–2·2 × sepals, very obliquely obovate; apiculus subacute; glands striiform and punctiform. *Stamens c.* 120, longest 6–8 mm long, *c.* 0·5 × petals. *Ovary* 2·5–3 × 1·5–2 mm, ellipsoid; styles 3, 4–5 mm long, *c.* 1·4 × ovary, spreading-incurved; stigmas small to narrowly capitate. *Capsule c.* 6 × 3·5 mm, ellipsoid, shorter than sepals. *Seeds* 1–1·2 mm long, ecarinate; testa finely reticulate-scalariform.





In subpáramo and páramo, most frequently in thickets; 2850–4100 m.



Map 6 9. *H. carinosum* ▲; 12. *H. lycopodioides* ○; 13. *H. thuyoides* •.

Colombia (Arauca, Boyacá, Cundinamarca), on the humid side of the Cordillera Oriental from Sierra Nevada del Cocuy to Páramo de Zipaquirá. Map 6.

COLOMBIA. Arauca: Sierra Nevada del Cocuy, Quebrada El Playon, Hoya San José, 3450 m, 9.vi.1973 (fl), *Cleef* 10117 (U). Boyacá: Sierra Nevada del Cocuy, Valle de San José, *c.* 4000 m, 10.ix.1957 (fl), *Grubb, Curry & Fernandez-Perez* 768 (COL, K, US); between Chitá and Sácama, Quebrada del Curial (La Porquera), 3350 m, 15.ix.1969 (fl), *Cuatrecasas & Laureano Rodriguez* 27787 (BM, COL, US). Cundinamarca: see type.

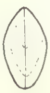
H. lycopodioides is morphologically and geographically intermediate between 10 *H. simonsii* and 13 *H. thuyoides*. It is very similar to the latter, differing essentially in the stiff, acute to acuminate leaves that give the shoots an *Araucaria*-like appearance.

13. **Hypericum thuyoides** Kunth

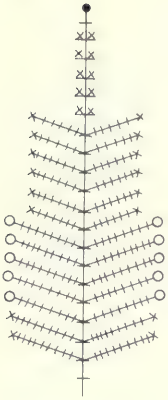
in Humboldt, Bonpland & Kunth, *Nova Gen. et Sp. Pl.* **5**: 187, t. 456 (1822); R. Keller in *Bull. Herb. Boissier* II, **8**: 177 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Gleason in *Bull. Torrey bot. Club* **56**: 101 (1929). Type: Colombia, Tolima?, Andes de Quindiu, entre Cartago et Ibagué, x.1805 (fl), *Humboldt & Bonpland* (P-HUM!, holotype; B-WILLD, P!, isotypes).

Brathys thuyoides (Kunth) Spach, *Hist. nat. vég.* Phan. **5**: 448 (1836), in *Annls Sci. nat.* (Bot.) II, **5**: 366 (1836).
H. hartwegii var. *patens* R. Keller in *Bull. Herb. Boissier* II, **8**: 182 (1908). Type: Colombia, Cundinamarca, mountains to the east of Bogotá (fl), *Holton* 785 (K!).
H. genistoides Kunth in sched.

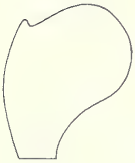
Icon: Humboldt, Bonpland & Kunth, *Nova Gen. et Sp. Pl.* **5**: t. 456 (1822).



Shrub or small tree (0·5–)1–3(?–6) m tall, spreading, with branches ascending, lateral, short (flowering) and long, narrowly spiciform to narrowly conical (extension), or rarely pseudo-dichotomous. *Stems* purplish-brown, 4-lined when young, eventually terete, without epidermal emergences, cortex exfoliating in strips; internodes 1·5–3 mm long. *Leaves* sessile, spreading to recurved, tetrastichous, persistent; lamina 2–8 × 1–2 mm, sometimes increasing in size along shoot, elliptic or rhombic-elliptic or elliptic-oblong to oblanceolate-spathulate or narrowly oblong, incurved-conduplicate, midrib prominent beneath or not, margin narrowly hyaline



and usually undulate, not glaucous, thinly chartaceous; apex acute to obtuse, cucullate, base cuneate to angustate or shortly pseudopetiolate, pairs united to form marked interfoliar ridge; basal vein 1, branched or usually unbranched; laminar glands ± dense, visible on both sides or above only. *Inflorescence* 1-flowered, terminal and on short lateral branches, the whole shoot cylindric to conic and sometimes racemiform due to retarded maturity of terminal flower, rarely with pseudo-dichotomous branches from node below; pedicel amost absent; upper leaves foliose. *Flowers* 20–30 mm in diam., stellate. *Sepals* 3–5 × 1·5–2·5 mm, oblong-lanceolate or elliptic to obovate-elliptic, acute to obtuse, margin narrowly hyaline; veins 9–11, not or scarcely branched, midrib apically incrassate; glands linear, punctiform distally. *Petals* bright yellow to orange-yellow, 10–17 × 6–11 mm, 3–4 × sepals, very obliquely obovate; apiculus obtuse; glands striiform with few distal dots. *Stamens* 100–120, longest 5–6 mm long, *c.* 0·4–0·5 × petals. *Ovary* 2–3 × 1–2 mm, ovoid to ellipsoid; styles 3, 4–7 mm long, *c.* 2 × ovary, spreading; stigmas scarcely to narrowly capitate. *Capsule c.* 3·5 × 2 mm, ellipsoid, shorter than sepals. *Seeds* not seen.



In scrub and thickets on slopes of the páramo; especially in boggy areas; 2500–3600 m.

Colombia (Boyacá, Cundinamarca, Tolima?, Meta); mainly in the mountains around Bogotá. Map 6.

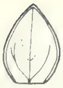
COLOMBIA. Boyacá: Sogamosa to Pajarito, near Km 268, *c.* 2500 m, 27.viii.1953 (fl), *Langenheim* 3601 (COL). Cundinamarca: Bogotá to Choachi, 30 km, Páramo de Cruz Verde, 3050 m, 8.viii.1974 (fl), *Grabandt & Idrobo* 219 (COL); Municipio de La Calera, Páramo de La Siberia, 3000–3500 m, 25.x.1953 (fl), *Humbert et al.* 26890 (COL, P, S) Meta: Páramo de Sumapaz, Hoya Sitiales, 300 m an al NW. de la Laguna La Primavera, 3580 m, 25.: 72 (fl), *Cleef* 985 (COL, U). Tolima?: see type.

H. thuyoides is a rather variable species with a restricted distribution in central Colombia, records from Nariño and northern Ecuador being errors for 20 *H. laricifolium* (q.v.).* It is easily distinguishable from typical *H. lycopodioides* by the thinner, usually undulate leaves, and from *H. laricifolium* by the denser habit and the usually broader or spathulate, undulate leaves with midrib not impressed beneath. 15 *H. myricariifolium*, with which it has been confused, has smaller, thicker, broader leaves and corky emergences near the top of the upper internodes, and the cortex exfoliates in irregular flakes.

Some specimens are very close in form to *H. lycopodioides* (e.g. *Humbert et al.* 26890). From these there are morphological trends in two directions: i) towards narrower leaves and narrower, spiciform shoots ('*H. genistoides*' in sched.) (e.g. *Langenheim* 3601); ii) towards broader, shorter leaves and broader, pyramidal shoots, thus approaching 14 *H. goyanesii* (e.g. *Grabandt & Idrobo* 219). Extreme forms of trend i) have been confused with *H. laricifolium*, which has thicker, more lucent leaves with midrib impressed.

14. **Hypericum goyanesii** Cuatrec.

[in *Trab. Mus. nac. Cienc. nat. Jard. bot. Madrid* (Bot.) no. 27: cuadro 7 inter 54 et 55 (1934), nomen] in *op. cit.*, no. 29: 9 (1935), *op. cit.*, no. 33: 83, f. 1A (1936). Type: Colombia, Cundinamarca, Guasca, Los Gaques wood, 3000 m, 24.iv.1932 (fl), *Cuatrecasas* 3229 (MA, holotype; K!, isotype).



Shrub 1–3 m tall, spreading, with branches ascending to divergent or pendent, lateral, short (flowering) and long (extension), not pseudo-dichotomous. *Stems* reddish-brown, 4-lined and ancipitous when young, sometimes wrinkled, eventually terete, cortex exfoliating in irregular flakes; internodes 2–8 mm long. *Leaves* sessile, spreading to deflexed, tetrastichous; lamina 2–5·5 × 1·5–3·5 mm, increasing in size along shoot, oblong-ovate or ovate to triangular-ovate or subcircular, incurved-conduplicate or saccate, with midrib slightly prominent beneath or not, margin narrowly hyaline, not glaucous, chartaceous, deciduous almost at the base after turning brown, leaving narrow basal ring; apex subacute or apiculate-obtuse to rounded, base cordate-amplexicaul, pairs ± perfoliately united; basal vein 1, sometimes with 1–2 pairs of near-basal branches, rarely with visible tertiary reticulum; laminar glands dense to rather few, large, ± prominent on both sides. *Inflorescence* 1-flowered, terminal and on short lateral branches, the whole shoot cylindric to conical, without pseudo-dichotomous branches; pedicel 1–3·5 mm long; upper leaves foliose. *Flowers* 20–40 mm in diam., stellate. *Sepals* 5–8 × 2–3·5 mm, the outer oblong to ovate, often cordiform, the inner oblong to lanceolate, acute or obtuse to rounded, cucullate; margin narrowly hyaline; veins 7–11, branching and anastomosing distally, midrib distally incrassate; glands linear, distally punctiform. *Petals* bright yellow, 10–20 × 6–12 mm, 2–2·5 × sepals, obovate; apiculus obtuse; glands striiform and punctiform. *Stamens c.* 120–150, longest 5–6 mm long, *c.* 0·4–0·5 × petals. *Ovary* 2·5–3 × 1·5 mm, narrowly ovoid; styles 3, 5–8 mm long, *c.* 2–2·5 × ovary, spreading-incurved; stigmas narrowly capitate. *Capsule* 5–6 × 4 mm, broadly ellipsoid to subglobose, equalling or exceeding sepals. *Seeds c.* 1 mm long, ecarinate; testa finely scalariform-reticulate.

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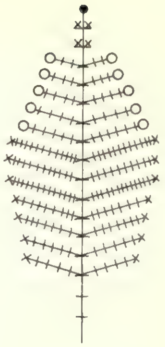
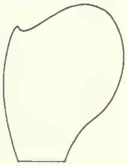
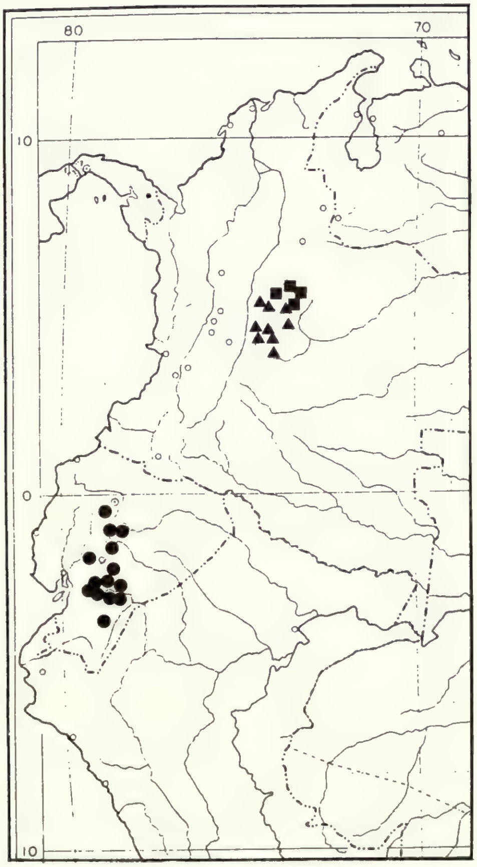
* Knuth's record from Venezuela, Mérida, Páramo de Timotes (*Jahn* 847) (*Reprium Spec. nov. Regni veg.* Beih. **43**: 484 (1927)) must be a misidentification, but I have not seen the specimen.





In degraded forest and scrub on open slopes and banks in the páramo and subpáramo, mainly near water and sometimes in pure stands (Lozano-C. & Schnetter (1976)); 2730–3590 m.

Colombia (Cundinamarca, Meta). Map 7.



Map 7 14. *H. goyanesii* ▲; 16. *H. cuatrecasii* ■; 17. *H. quitense* •.

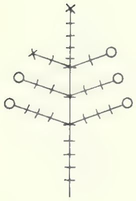
COLOMBIA. Cundinamarca: Páramo de Guasca, 3300 m, 16.xii.1938 (fl), *Balls* 5764 (BM, COL, K); Páramo de Zipaquirá [Guerrero], between Zipaquirá and Pacho, 3100–3200 m, 16.vi.1940 (fl), *Cuatrecasas* 9526 (COL, F, P); Páramo de Cruz Verde, fondo del valle al sur de La Viga, 3590 m, 28.viii.1972 (fl), *Cleef* 3287 (BM, COL, U). Meta: Macizo de Sumapaz, alredores de la Laguna La Guitarra, 3380–3420 m, 4.vii.1981 (fl & fr), *Díaz* 2398 (COL).

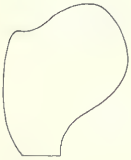
H. goyanesii resembles *H. thuyoides* (which occurs in the same area) but differs in, for example, the thicker, saccate, cordate-amplexicaul leaves that become deflexed when withering, the spreading habit, and the exfoliation of the cortex in flakes rather than strips. It is related to both *H. thuyoides* and 16 *H. cuatrecasii*.

15. **Hypericum myricariifolium** Hieron.

in *Bot. Jahrb.* **21**: 321. (1895); R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Gleason in *Bull. Torrey bot. Club* **56**: 102 (1929). Type: Colombia, Cundinamarca, Páramo de Pasca, 3700–3800 m, vi.1868? (fl), *Stübel* Colomb. 124 (B†, holotype; F!, NY!, photographs).

H. myricariifolium Hieron. ex R. Keller in *Bot. Jahrb.* **42**: 130 (1908), in *Bull. Herb. Boissier* II, **8**: 178 (1908). Type: as for *H. myricariifolium* Hieron.
H. lindenii sensu Cuatrec. in sched., non R. Keller.





Shrub up to 2 m tall, bushy or with branches ascending to spreading or prostrate and matted, lateral, short (flowering) or long and narrowly conical (extension), rarely pseudo-dichotomous. *Stems* orange-brown, 4-lined when young, sometimes wrinkled or with corky emergences especially near flowers, eventually terete, cortex exfoliating in irregular flakes; internodes 1·4–6 mm long. *Leaves* sessile, imbricate to spreading, tetrastichous, cupressoid; lamina 1–3·5 × 0·7–2(–2·6) mm, triangular-ovate to oblong-ovate, incurved-cucullate, with midrib plane or usually impressed beneath, margin relatively broadly hyaline, not glaucous, coriaceous; apex subacute to obtuse, base rounded to cordate-amplexicaul, pairs shortly united; basal vein 1, unbranched, without visible tertiary reticulum; laminar glands dense to few, large, prominent beneath or not. *Inflorescence* 1-flowered, not terminal, on short lateral branches, the whole shoot narrowly conical, racemiform, rarely with a pseudo-dichotomous branch; pedicel 1–1·5 mm long; upper leaves foliose. *Flowers* 18–25 mm in diam., stellate. *Sepals* 4–5 × 1·7–2·7 mm, the outer ovate, sometimes cordiform, the inner ovate-lanceolate to lanceolate-oblong, acute to rounded, cucullate, margin narrowly to rather broadly hyaline; veins 9–11, usually unbranched, midrib not prominent beneath; glands linear to punctiform. *Petals* bright (?) yellow, 10–15 × 6–9 mm, *c.* 2·2–3 × sepals, obovate; apiculus rounded; glands striiform and punctiform. *Stamens* 60–80, longest 5–6 mm long, *c.* 0·35–0·5 × petals. *Ovary* 2–3 × 1–1·5 mm, narrowly ovoid-ellipsoid; styles 3, 5–7 mm long, *c.* 2–2·5 × ovary, spreading-outcurved; stigmas narrowly capitate. *Capsules* 5 × 4 mm, broadly ellipsoid, exceeding sepals. *Seeds* not seen.

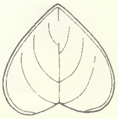
On open slopes in the páramo; 3000–4120 m.

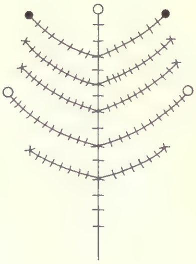
Colombia (Cundinamarca); in the higher páramos near Bogotá. Map 8 (p. 44).
COLOMBIA. Cundinamarca: Cordillera Oriental S. of Usmé, Páramo de Chisacá, *c.* 4120 m, 9–11.xi.1958 (fl), *Barclay & Juajibioy* 6178 (COL, MO, NY); Macizo de Sumapaz, Andabobos, 3760–3720 m, 8.i.1969 (fl), *Cuatrecasas & Jaramillo* 27031 (BM, US); Páramo de Cruz Verde, W. slopes, 3150 m, 7.x.1938 (fl), *Cuatrecasas* 409 (COL, F, P).

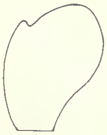
H. myricariifolium was formerly though to be inseparable from *H. thuyoides* (see Cuatrecasas, 1936: 83). However, it can be distinguished *inter alia* by the thick, broad-based, cucullate leaves with a broad hyaline margin and large glands. Its nearest relative is *H. goyanesii*, the area of which includes that of *H. myricariifolium*. It is clearly a high-altitude derivative of *H. goyanesii*, and the altitudinal ranges of the two taxa overlap from 3000–*c.* 3600 m; there is no evidence of hybridization between them. They can be distinguished by the leaf shape (see key), which gives the young shoots of *H. myricariifolium* a cupressoid appearance lacking in *H. goyanesii*, the leaf aspect (leaves becoming reflexed in *H. goyanesii* but no more than spreading in *H. myricariifolium*), and usually by the leaf size. It seems advisable, therefore, to recognize them as species, despite their overlapping ranges.

16. **Hypericum cuatrecasii** Gleason

in *Revta Acad. Colomb.* **5**: 38 (1942), in *Bull. Torrey bot. Club* **70**: 174 (1943). Type: Colombia, Boyacá, Cordillera Oriental, between Arcabuco and Tunja, 2950 m, 5.viii.1940 (fl), *Cuatrecasas* 10439 (NY!, holotype; COL, F!, P!, U!, US!, isotypes).







Shrub up to 2 m tall, spreading, with branches divergent, lateral, ± short (flowering) and long (extension), or pseudo-dichotomous. *Stems* yellow to reddish-brown, 4-lined and ancipitous when young, eventually terete, without epidermal wrinkles or emergences, cortex exfoliating in strips or flakes; internodes 2–5 mm long. *Leaves* sessile, spreading to deflexed, obscurely tetrastichous, deciduous almost at the base after turning brown, leaving narrow basal ring; lamina (2–)4–7 × (2–)3–7 mm, gradually increasing in size along shoot, broadly ovate to subcircular, plane or slightly saccate, with midrib prominent beneath, margin not or very narrowly hyaline, not glaucous, coriaceous; apex acute to rounded, base cordate-amplexicaul, shallowly sheathing, pairs perfoliately united; basal or near-basal veins 1–3, with midrib branching, tertiary reticulum obscure; laminar glands dense to sparse, large, not prominent. *Inflorescence* 1-flowered, terminal and on short lateral shoots, the whole shoot ± cylindrical, sometimes with pseudo-dichotomous branches; pedicel 4–7 mm long; upper leaves foliose. *Flowers c.* 20 mm in diam., stellate. *Sepals* 5–7 × 3–4 mm, the outer ovate, subcordiform, the inner ovate-oblong, subacute to rounded, cucullate, margin narrowly to broadly hyaline; veins 7–11, obscurely branching, midrib not prominent; glands linear, distally punctiform. *Petals* (bright?) yellow, 9–12·5 × 6·5–7·5 mm, *c.* 1·8 × sepals, obliquely obovate; apiculus obtuse; glands mostly striiform, distally punctiform. *Stamens c.* 120–150, longest 5–6 mm long, *c.* 0·5 × petals. *Ovary* 2·5–3 × 1·5–2 mm, broadly ovoid; styles 3(4), 5–6·5 mm long, 2 × ovary, spreading-incurved; stigmas scarcely to narrowly capitate. *Capsule c.* 6 × 3·5 mm, ellipsoid, slightly exceeding sepals. *Seeds* not seen.

In páramo and degraded forests; 1990–3000 m.

Colombia (Boyacá, Santandér), in the Páramo de Arcabuco. Map 7 (p. 39).

COLOMBIA. Boyacá: Sáchica, 1990 m, viii.1964, *Saravia* 4425 (COL). Santandér: Cerro Berlin, between Arcabuco and La Palma, 2900 m, 28.iii.1973 (fr), *Cuatrecasas, Garcia-Barriga & Jaramillo* 28668 (BM, COL, US).

H. cuatrecasii is most closely related to 14 *H. goyanesii*, from which it is separable by the more spreading habit, and by leaf size and shape, the absence of pellucid leaf margins, smaller flowers, and shorter styles. It appears to be restricted to extreme eastern Boyacá as far as the border with Santandér.

17. **Hypericum quitense** R. Keller

in *Bull. Herb. Boissier* II, **8**: 182 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Gleason in *Bull. Torrey bot. Club* **56**: 102 (1929). Type: Ecuador, Azuay, near Cuenca, Surucucho, viii.1865 (fl), *Jameson* 128 (W!, holotype; K!, isotype).

H. rimbachianum Diels in *Biblthca bot.* **116**: 108 (1937). Type: Ecuador, Cañar, N. of Biblian, *c.* 3400 m, 13.viii.1933, *Diels* 497 (B†, holotype).

Icon: Fig. 7.

Shrub or shrublet 0·3–1(–1·5) m tall, erect or spreading, with branches divergent, lateral, short (flowering) and long (extension), not pseudo-dichotomous. *Stems* reddish-brown, 4-lined and markedly ancipitous when young, eventually terete, without wrinkles or corky emergences, cortex exfoliating in flakes; internodes 4–10

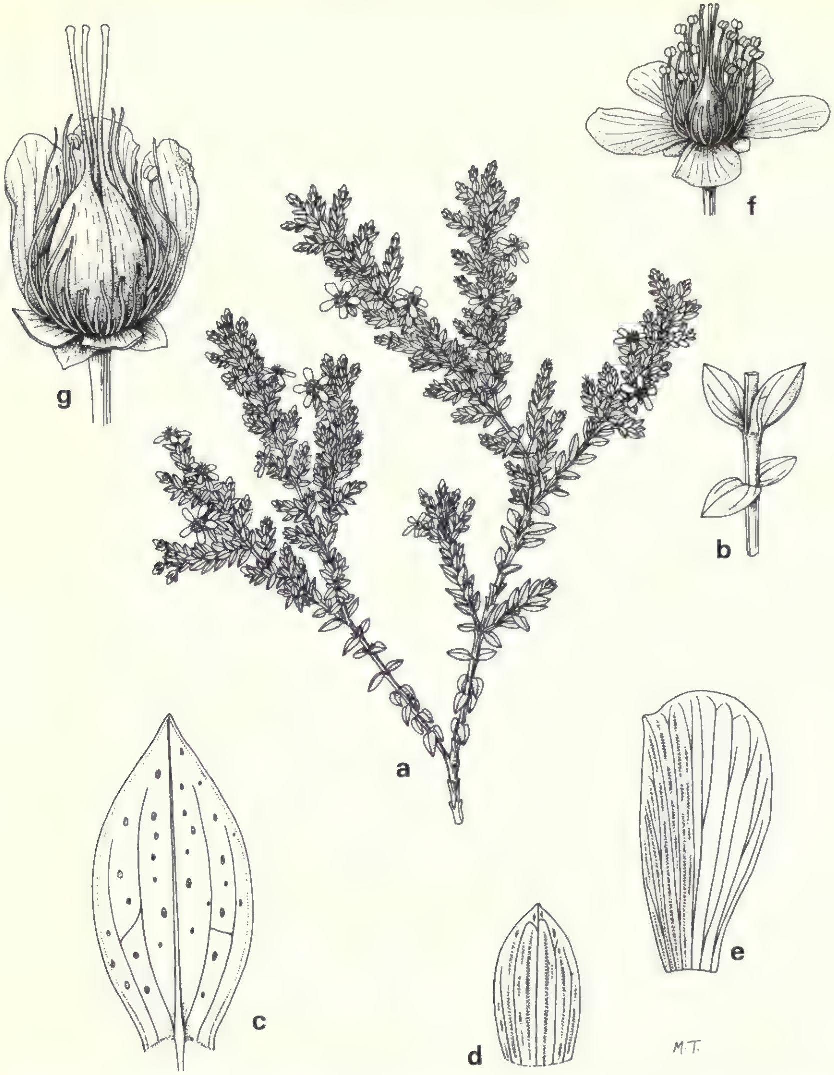
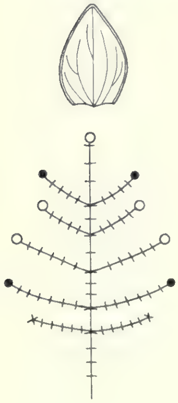


Fig. 7 *H. quitense*: (a) habit; (b) stem with leaves; (c) leaf; (d) sepal; (e) petal; (f) stamens (partly cut away) and ovary; (g) capsule (a × ½; b, f, g × 4; c–e × 6). All *Camp* 4133.



mm long. *Leaves* sessile, spreading to deflexed, obscurely tetrastichous, turning brown, deciduous with the cortex; lamina 4–9·5 × 2·5–5 mm, sometimes increasing in size along shoot, oblong (lower) to broadly ovate, plane or slightly saccate or conduplicate, midrib prominent beneath, margin narrowly hyaline, otherwise pale green but not or only slightly glaucous, subcoriaceous; apex acute (lower) to obtuse, base broadly cuneate, pairs shortly united; basal or near-basal veins 3(5), with laterals and sometimes midrib branching, tertiary reticulum obscure or apparently absent; laminar glands mainly peripheral, dense, rather large, not prominent. *Inflorescence* 1-flowered, terminal and on very short lateral shoots, the whole shoot narrowly cylindrical, without pseudo-dichotomous branches; pedicel 3–7 mm long; upper leaves foliose. *Flowers* 8–12 mm in diam., stellate. *Sepals* 5 × 1–2 mm, elliptic to narrowly oblong, the outer sometimes broader, apiculate-obtuse to acute, subcucullate, margin narrowly hyaline; veins 3–5, not or scarcely branching, all prominent; glands all linear or distally punctiform. *Petals* bright yellow, 5–6·5 × 3–4 mm, 1·5–2 × sepals, obovate; apiculus subacute to obtuse; glands few, striiform and

punctiform. *Stamens* 30–45, longest 3–4 mm long, *c.* 0·65 × petals. *Ovary* 1·5–2 × 0·7–1 mm, narrowly ovoid; styles 3, 3–4 mm long, *c.* 2 × ovary, spreading; stigmas broadly capitate. *Capsule* 3–4·5 × 2·5–3·5, ellipsoid, equalling or slightly exceeding sepals. *Seeds c.* 0·7 mm long, ecarinate, testa finely scalariform.

In damp meadows of the páramo; 2600–3800 m.

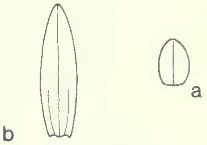
Ecuador (Bolivar, Tungurahua, Cañar, Azuay). Map 7 (p. 39).

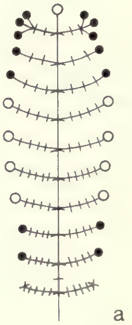
ECUADOR. Tungurahua: around Lago Pisayambo, 3800 m, 26.xii.1964 (fl), *Knight* 268 (BM). Bolivar: Cordillera Occidental, Pucará de Telimbela, 2600–3000 m, 18.xi.1943 (fl), *Acosta Solis* 6825 (F). Cañar: near Pimo, 3060–3120 m, 9.vii.1945 (fl), *Camp* E-4133 (BM, NY). Azuay: mountains above Sayausid, 3000–3200 m, 18.iii.1974 (fl & fr), *Harling & Anderson* 12630 (GB).

H. quitense is related to *H. cuatrecasii* but is much smaller in all parts.

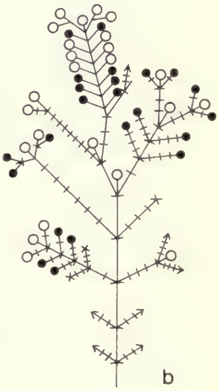
18. **Hypericum loxense** Bentham

Pl. Hartweg.: 126 (1843); R. Keller in *Bull. Herb. Boissier* II, **8**: 177 (1908), in Engler & Prantl, *Nat. Pfanzenfam.* 2nd ed. **21**: 181 (1925); Gleason in *Bull. Torrey bot. Club* **56**: 102 (1929). Type: Ecuador, Loja, 'in montibus Loxa', viii.1842? (fl & fr), *Hartweg* 720 (K!, holotype; BM!, F!, P!, isotypes).





Shrub or shrublet, 0·2–1(–1·5) m tall, erect or decumbent to prostrate, with branches ascending to strict, lateral, short (flowering) and long (extension), not pseudo-dichotomous. *Stems* reddish-brown, 4-lined and ancipitous when young, eventually terete, without wrinkles or emergences, cortex exfoliating in irregular flakes or strips; internodes 1·5–10 mm long. *Leaves* sessile, erect, imbricate and sometimes markedly tetrastichous when young, spreading and turning brown, deciduous with the cortex (or sometimes breaking off earlier); lamina 2–10 × 0·6–3 mm, not increasing in size along shoot, narrowly oblong or oblanceolate or linear to triangular-lanceolate or triangular-ovate, incurved-conduplicate or subsaccate, midrib prominent beneath or not, margin narrowly hyaline, not or slightly glaucous, subcoriaceous to chartaceous; apex acute to obtuse, base narrowly cuneate or parallel-sided to broadly cuneate or truncate, pairs shortly united; basal veins 1(3–5), with midrib sometimes branching, tertiary reticulum rarely present; laminar glands dense to rather sparse, varying in size, prominent or not. *Inflorescence* either (i) wholly 1-flowered, terminal and on very short lateral shoots, the whole shoot narrowly cylindric, with lateral branches sometimes also bearing flowering branches but rarely with pseudo-dichotomous branches, or (ii) 1–*c.* 15-flowered in terminal and sometimes lateral dichasia or mixed dichasia and pseudo-dichotomies; peduncle and pedicels 2–9 mm long; upper leaves foliose. bracts gradually smaller. *Flowers* 6–10 mm in diam., stellate. *Sepals* 1·5–5·3 × 0·5–1·6 mm, elliptic or lanceolate to narrowly oblong, the outer sometimes broader, apiculate-obtuse to acute, sometimes cucullate, margin narrowly hyaline; veins 3–5, not or scarcely branching, not or only the midrib slightly prominent; glands all linear or distally punctiform. *Petals* pale or bright yellow to orange, darker or reddish in bud, 3–6(–7·5) × 1·5–3 mm, 1·5–2 × sepals, obovate; apiculus obtuse or obsolete; glands few, striiform and punctiform. *Stamens* 20–40, longest 2–4 mm long, *c.* 0·65 × petals. *Ovary* 0·7–1·5 × 0·5–1 mm, narrowly ovoid; styles 3(4), 1·3–3 mm long, 1·3–2 × ovary, spreading; stigmas ± broadly capitate. *Capsule* 2·5–4 × 1·5–2·2 mm, ellipsoid or ovoid-ellipsoid, equalling sepals. *Seeds* 0·7–0·8 mm long, ecarinate, testa finely scalariform.

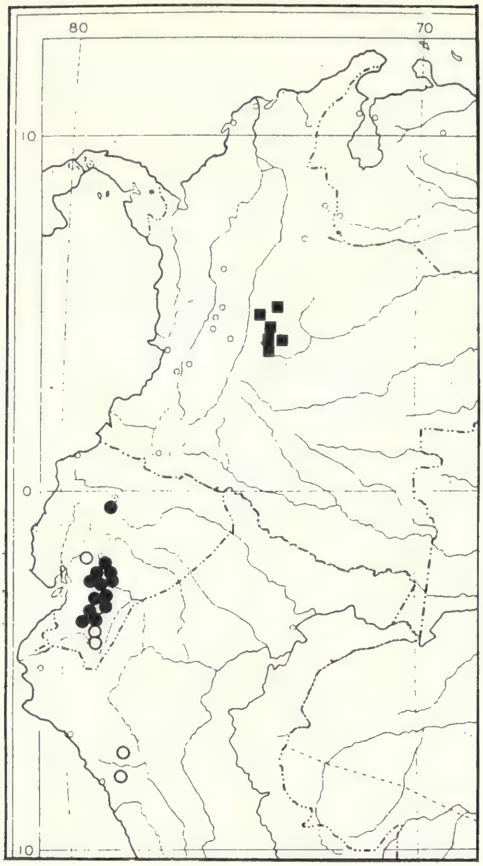


On dry slopes and in rocky places in the páramo; 2350–3800 m.

Ecuador (Cotopaxi, Chimborazo, Cañar, Azuay, Loja), Peru (Cajamarca, La Libertad). Map 8.

H. loxense is closely related to *H. quitense*, which although overlapping it in distribution is apparently ecologically distinct. In addition, *H. loxense* has narrower and/or smaller leaves and usually smaller flowers.

H. loxense comprises two populations of which subsp. *aequatoriale* is nearer to *H.*



Map 8 15. *H. myricariifolium* ■; 18. *H. loxense*: a. subsp. *aequatoriale* ●, b. subsp. *loxense* ○.

quitense. The most primitive form of this subspecies is from Mt. Corazón (Cotopaxi), where it is geographically isolated from the rest (Chimborazo to Loja). It is always erect and has incurved-cucullate, relatively broad leaves. Subsp. *loxense* differs in having relatively narrow, plane leaves and a usually laxer and more spreading habit. Its most primitive form occurs in Loja, whence there is (i) a southern trend (with disjunction) to Peru (Cajamarca, La Libertad) in which the leaves become smaller and narrower, and (ii) a northern trend (Azuay, Cañar, Chimborazo) towards prostrate weak stems and somewhat smaller leaves. The occurrence of intermediates in Loja prevents the recognition of these taxa as species.

18a. **Hypericum loxense** subsp. **aequatoriale** (R. Keller) N. Robson, **stat. nov.**

H. loxense var. *aequatoriale* R. Keller in *Bot. Jahrb.* **42**: 129 (1908), in *Bull. Herb. Boissier* II, **8**: 181 (1908). Type: Ecuador. Cañar, between Azogues and Páramo de Huairacaja, 2700–3000 m, ix–x.1905? (fl & fr), *Lehmann* 4795 (B†, holotype, F!, photograph; F!, K!, US!, isotypes).

Leaves usually erect and ± densely imbricate; lamina 2·5–5·2 × 1–2 mm, lanceolate or rarely oblong to broadly triangular-ovate, plane to subsaccate, chartaceous to subcoriaceous, apex acute to obtuse, base ± broadly cuneate to truncate, midrib rarely prominent beneath. *Inflorescence* branches 1–3-flowered. *Sepals* 2–3 × 0·5–1·1 mm, narrowly oblong to lanceolate, acute to subacute.

Ecuador (Cotopaxi, Chimborazo, Cañar, Azuay, Loja).

ECUADOR. Cotopaxi: Corazón, 3200 m, 22.vi.1876, *André* K. 436 (K). Chimborazo: Páramo de Cachenco, *c.* 3800 m, 27.vii.1959 (fl), *Barclay & Juajibioy* 8258 (NY). Cañar: near Pimo, 3060–3120 m, 9.vii.1945 (fl), *Camp* E-4136 (BM, NY); Tipococha, 3400 m, 9.vii.1939 (fl & fr), *Penland* 994 (F). Azuay: Beños, SW. of Cuenca, *c.* 2700 m, 12.v.1974 (fl), *Harling & Anderson* 14561 (GB); San Miguel to Cuenca, 25 km, 3000 m, 15.ix.1969, *B. & C. Maguire* 61712 (BM, NY). Loja: between Loja and Cuenca, *c.* 20 km N. of Saraguro, 3080 m, 21.x.1980 (fl & fr), *Croat* 50854 (BM, MO).

18b. **Hypericum loxense** subsp. **loxense**

Leaves spreading or more rarely erect and subimbricate; lamina 4–10 × 0·6–3 mm, narrowly oblong or narrowly elliptic or rarely oblanceolate to linear, plane to incurved, chartaceous, apex acute to rarely subacute, base narrowly cuneate to parallel-sided, midrib often prominent beneath. *Inflorescence* branches usually dichasial or mixed, more rarely 1-flowered. *Sepals* 2–4·5(5·3) × 0·5–1·2(1·6) mm, narrowly elliptic to oblong, acute.

Ecuador (Chimborazo, Cañar, southern Azuay, Loja), Peru (Cajamarca, La Libertad).

ECUADOR. Azuay: Páramo Portete, 3600 m, 13.iii.1953 (fl), *Prescott* 793 (NY). Chimborazo: Urbina, towards Mt. Chimborazo, *c.* 3700 m, 27.vii.1939 (fl & fr), *Asplund* 7913 (S). Cañar: near El Tambo (*c.* 69 km S. of Sibombé), 2850–3000 m, 5.vii.1945 (fr), *Camp* E-4000 (BM, NY). Loja: Loja, S. of the town, *c.* 2350 m, 4.x.1955 (fl & fr), *Asplund* 17919 (S); between Cuenca and Loja, near Uña, 1865 (fl & fr), *Jameson* 127 (K, W).

PERU. Cajamarca: above Sunchubamba, 3680 m, 8.vi.1957 (fl), *Ellenberg* 1862 (U). La Libertad: Playapampa, *c.* 2700 m, 15–24.vi.1923 (fl), *Macbride* 4525 (NY).

The disjunct populations in Chimborazo and northern Azuay differ in their decumbent to prostrate habit, whereas the collection from Cajamarca differs in having oblanceolate subacute leaves and somewhat larger flowers than normal.

19. **Hypericum sabiniforme** Trev.

Hyper. Animad.: 15 (1861); Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 296 (1862) ['*sabinaeforme*']. Type: Colombia, Boyacá, Prov. de Tunja, Soatá, 1300 m, iv.1843 (fl), *Linden* 1328 (BHU?, holotype; BM!, GH!, K!, P!, W!, isotypes).

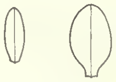
Hypericum thymifolium sensu Turcz. in *Bull. Soc. Nat. Moscou* **31** (1): 386 (1858), non Banks & Solander (1794) nec Kunth (1822).

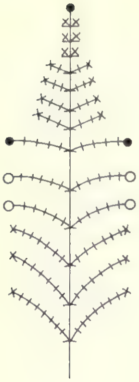
Hypericum hartwegii sensu Triana & Planchon, *tom. cit.*: 295. (1862) pro parte, excl. typum; R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* **3** (6): 214 (1893) pro parte, excl. typum, in *op. cit.*, 2nd ed., **21**: 181 (1925) pro parte quoad specim. Colomb.

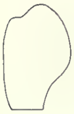
Hypericum lindenii R. Keller in *Bull. Herb. Boissier* II, **8**: 183 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Gleason in *Bull. Torrey bot. Club* **56**: 102 (1929). Type: Colombia (as for *H. sabiniforme*), *Linden* 1328 (W!, holotype; BM!, GH!, K!, P!, isotypes).

Hypericum trianae N. Robson in Cleef, *Veg. Páram. Colomb. Cord. Or.*: 164, 305 (1981), nomen.

Shrub 0·3–0·5 m tall, erect, bushy, with branches erect, ± strict, lateral or rarely pseudo-dichotomous. *Stems* orange-brown, 4-lined when young, eventually terete, cortex exfoliating in strips; internodes 1·5–4 mm long. *Leaves* sessile or with pseudopetiole up to 1 mm long, outcurving to appressed, loosely to densely imbricate, sometimes markedly tetrastichous, deciduous at or sometimes slightly above the base; lamina 1·5–7 × 0·4–3 mm, ovate or elliptic to oblanceolate or narrowly oblong, ± cucullate, incurved, with margin narrowly hyaline, midrib impressed beneath, concolorous, glaucous, coriaceous, markedly papillose or subpapillose above, less so beneath; apex obtuse to rounded, base cuneate-







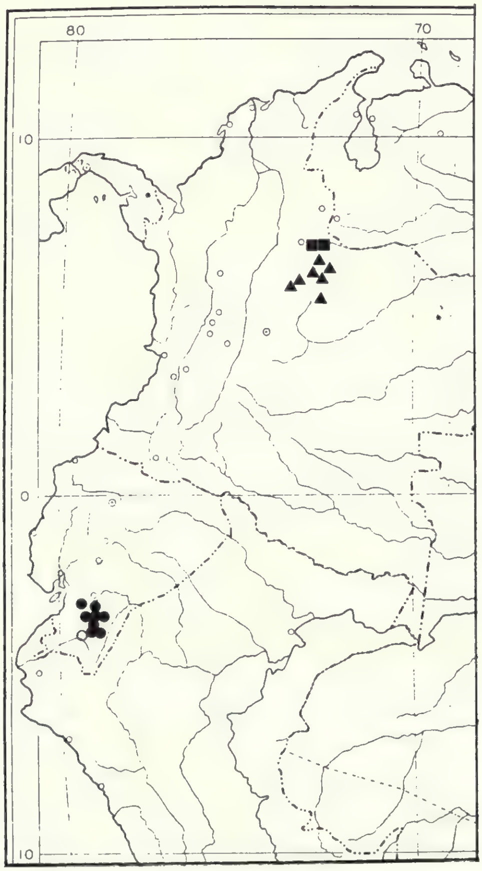
pseudopetiolate to angustate or parallel, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense, large, not or slightly prominent. *Inflorescence* 1-flowered, terminal and on lateral branches; pedicel 1–2 mm long; upper leaves transitional or foliose. *Flowers* 5–20 mm in diam., stellate. *Sepals* 2–5 × 0·5–3 mm, ovate-oblong to oblong, obtuse to rounded, plane or ± cucullate, margin narrowly hyaline; veins 3–9, unbranched, with midrib prominent beneath or not; glands mostly linear to mostly punctiform. *Petals* bright (?) yellow, 4–11 × 2–6 mm, 2–2·5 × sepals, oblong-obovate; apiculus acute; glands distally interupted to wholly punctiform. *Stamens* 60–125, longest 2·5–4·5 mm long, 0·4–0·65 × petals. *Ovary* 1·5–2 × 0·8–1 mm, ovoid to ellipsoid-subglobose; styles 2, 1·5–5 mm long, 1–2 × ovary, ± spreading-outcurved; stigmas small. *Capsule* 3–5 × 2·5 mm, ovoid-cylindric to ellipsoid, exceeding sepals. *Seeds* not seen.

In dry páramo; 2000–3870 m.

Colombia (Boyacá). Map 9.

COLOMBIA. Boyacá: Municipio de Susacón, páramo de Guantiva, 3140 m, 8.viii.1958 (fl), *Jaramillo & Hernández* 965 (US); NW. of Belen, Quebrada Minas, Hoya Clla. Larga, 3870 m, 25.ii.1972 (fl), *Cleef* 1807 (COL; U); 1 km E. of Vado Hondo, Valle de Rio Cusiara, 2915 m, 31.iii.1973 (fl). *Cleef, Cuatrecasas & Jaramillo* 9236B (COL); Páramo de Güina, 3200 m, 17.vii.1940 (fl), *Cuatrecasas & Garcia Barriga*. 9790 (F); Andes de Bogotá, 2500–3000 m, (fl), *Triana* s.n. (BM).

The type of *H. sabiniforme*, which superficially resembles a species of the African ericaceous genera *Philippia* or *Blaeria*, represents the extreme form of an eastward



Map 9 19. *H. sabiniforme* ▲; 22. *H. hartwegii* ○; 23. *H. maguirei* ●; 25. *H. gleasonii* ■.

cline. At the western end of the cline is a form with much larger ovate to elliptic pseudopetiolate leaves, markedly papillose above, and much larger flowers. Variation along the cline, however, appears to be continuous. The western form is near the broad-leaved form of *H. thuyoides*, but differs in having thicker, glaucous leaves with undulate to papillose epidermis.

Wood 3682 (Cundinamarca, between Neusa and San Cayetano) is intermediate between 13 *H. thuyoides* 'genistoides' (see p. 38) and 19 *H. sabiniforme*.

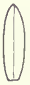
20. **Hypericum laricifolium** Juss.

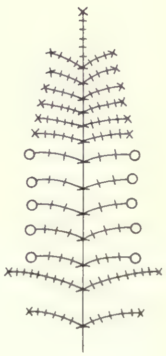
in *Annls Mus. Hist. nat. Paris* **3**: 160, t.16 f.1 (1804); Choisy, *Prodr. monogr. fam. Hypéric.*: 58 (1821), in DC., *Prodr. syst. nat. regni veg.* **1**: 553 (1824); R. Keller in *Bull. Herb. Boissier* **6**: 257 (1898), in *op. cit.* II, **8**: 176 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Kunth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 483 (1927). Type: Peru, without precise locality or date (fl), *J. de Jussieu** in Herb. A. L. de Jussieu 11800 (P – JUSS!, holotype; C!, F!, P!, isotypes).

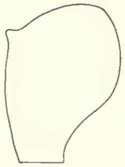
H. acerosum Kunth in Humboldt, Bonpland & Kunth, *Nova Gen. et Sp. Pl.* **5**: 187, t. 457 (1822). Type: Ecuador, Azuay, 'in Andium Assuay Quitensium', 3240 m, vii.1805 (fl), *Humboldt & Bonpland* (P-HUM!, holotype; P!, isotype).
Brathys laricifolia (Juss.) Spach, *Hist. nat. vég. Phan.* **5**: 366 (1836).
B. acerosa (Kunth) Spach, *Hist. nat. vég.* Phan. **5**: 449. 1836, in *Annls Sci. nat.* (Bot.) II, **5**: 366 (1836).
Hypericum laricifolium var. *acerosum* (Kunth) Weddell, *Chloris Andina* **2**: 271 (1857).
H. platypetalum Turcz. in *Bull. Soc. Nat. Moscou.* **31** (i): 388 (1858), non (Webb) Steudel (1840). Type: Ecuador, Pichincha, Quito, 1836? (fl), *Jameson* 60 (LE, holotype; BM!, K!, W!, isotypes).
H. racemulosum Turcz. in *Bull. Soc. Nat. Moscou.* **36** (1): 580 (1863). Type: Peru. Amazonas, Chachapoyas, 1835 (fl), *Mathews* 1611 (LE, holotype; BM!, KW!, P!, isotypes).
H. laricoides Gleason in *Bull. Torrey bot. Club* **56**: 104. (1929). Type: Venezuela, Mérida, Páramo de Timotes, Páramos de Chachapos, 3800–4200 m, 24.i.1928 (fl), *Pittier* 12713 (US!, holotype; F!, K!, MO!, isotypes).

Icones: Cuatrecasas in *Trab. Mus. Nac. Cienc. Nat. Madrid* (Bot.), no. 27: t. 29 (1934); Humboldt, Bonpland & Kunth, *tom. cit.*: t. 457 (1822); Fig. 8A.

Shrub or small tree (0·1–)0·3–3(–6) m tall, bushy or lax and spreading, with branches erect to spreading, lateral, short (flowering) and long, narrowly to broadly conical (extension). *Stems* 4-lined when young, eventually terete, blackish-brown, without epidermal emergences, cortex exfoliating in strips or irregular flakes; internodes 1·5–5 mm long. *Leaves* sessile, spreading or erect, sometimes imbricate, not markedly tetrastichous, persistent; lamina (2–)3–6(–8) × 0·3–2·2 mm, narrowly elliptic or narrowly elliptic-oblong to acerose, conduplicate to incurved, with midrib impressed beneath, margin narrowly hyaline and plane or subundulate, not glaucous, chartaceous to coriaceous; apex subacute to obtuse, cucullate, base narrowly cuneate to angustate, loosely clasping or not, pairs united to form narrow interfoliar ridge; basal vein 1, not or obscurely branched; laminar glands dense, scattered or in 1 row, impressed, usually visible beneath only. *Inflorescence* 1-flowered, on short lateral branches, rarely branching pseudo-dichotomously; pedicel 1·5–5 mm long; upper leaves foliose. *Flowers* 15–25(–30) mm in diam., stellate. *Sepals* 3–7 × 0·7–2·2 mm, oblong or elliptic to narrowly ovate or lanceolate, subacute to acute, cucullate, margin hyaline; veins 7–9, not or scarcely branched, midrib distally incrassate; glands linear, distally punctiform. *Petals* bright golden yellow to orange-yellow, 7–14)–22) × 4–10 mm, 2–3 × sepals, very obliquely, obovate; apiculus obtuse; glands striiform and punctiform. *Stamens* 70–110, longest 4–7 mm long, *c.* 0·5 × petals. *Ovary* 2–3·5 × 0·8–1·5 mm, ellipsoid; styles 3, 4–9 mm long, 2–4·5 × ovary, spreading; stigmas scarcely to narrowly capitate. *Capsule* 4–7 ×







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* The only specimen in Herb. de Jussieu that could be type material is labelled 'Perou, 1780, *Dombey*.'

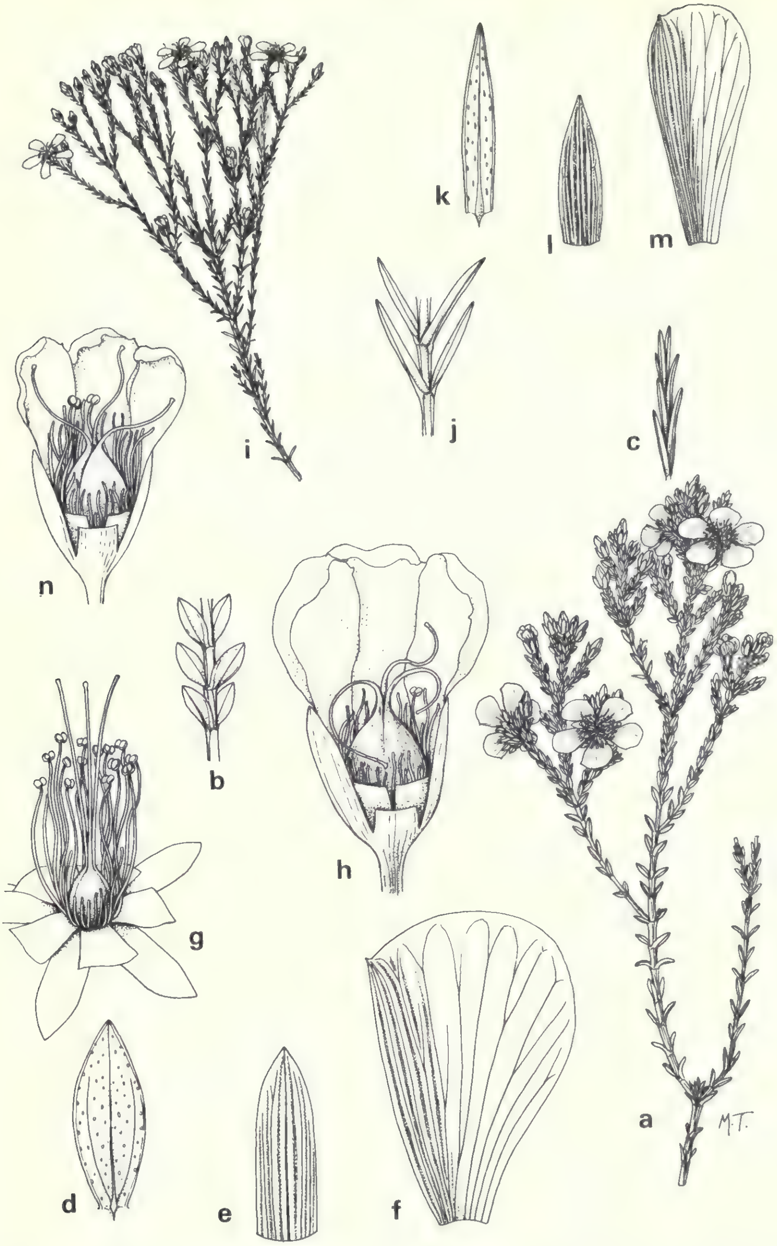


Fig. 8 A. *H. laricifolium*: (a) habit; (b) stem with leaves (Ecuador); (c) stem with leaves (Venezuela); (d) leaf; (e) sepal; (f) petals; (g) stamens (partly cut away) and ovary; (h) capsule. B. *H. martense*: (i) habit; (j) stem with leaves; (k) leaf; (l) sepal; (m) petal; (n) capsule (a, i × ½; b, c, j × 2; d–h, k–n × 4). A. *Luteyn* 6751 except (c) *Luteyn* 7583; B. *Seifriz* 421.

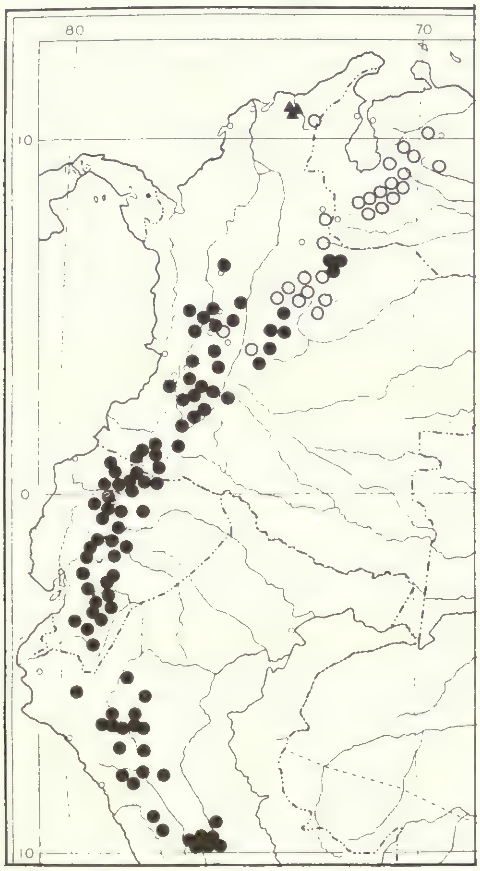
3–4 mm, ovoid to subglobose, equalling or exceeding sepals. *Seeds* 0·8–1 mm long, ecarinate; testa finely scalariform.

In the subpáramo and páramo, in open or more usually sheltered habitats, well-drained or not; 2200–4300 m.

From western Venezuela (Lara, Trujillo, Mérida, Zulia) along the Cordilleras

Central and Oriental of Colombia and Ecuador to central Peru (Huánuco, Ancash). Map 10.

COLOMBIA. Antioquía: between Medellin and Retiro, around Las Palmas, *c.* 2800 m, 16.x.1947 (st), *Gutiérrez, Barkley & Rosano* 24(F). Boyacá: Páramo La Rusia, NNW. of Duitama, 3550 m, 11.ix.1969 (fl & fr), *Cuatrecasas & Rodriguez* 27730 (BM, COL, US). Caldas: Río Otún, Nevado de Santa Isabel, Bagas de la Laguna Negra, 3800–3750 m, 24.xi.1946, *Cuatrecasas* 23160 (F, P, U). Cauca: Popayan, near Pitayo, 1841–1843 (fl), *Hartweg* 925 (BM, K, P, W); Páramo del Puracé, S. of the Volcán, San Francisco, 3450–3400 m, 23.vii.1943 (fl), *Cuatrecasas* 14571 (COL, F, P). César: Municipio de Valledupar, Corregimiento de Manaure, 2800 m, n.d. (fl), *Rodriguez* s.n. (COL). Chocó: Macigo de Tatamá, valle El Encanto, 3420 m, 13.ii.1983 (fl), *Cleef & Salamanca* s.n. (COL). Cundinamarca: Páramo de Guasca, vicinity of Bogotá, 3150 m, 23.viii.1959 (fl), *B. & C. Maguire* 44029 (BM, NY); Páramo de Palacio, Lagunas de Buitrago, 3550 m, 27.iv.1973 (fl), *Cleef* 9577 B (COL). Magdalena: Sierra de Perijá, plain between Cerro Venado and Cerro Avión, 3270–3350 m, 8.xi.1959 (fl), *Cuatrecasas & Romero-Castañeda* 25128 (COL). Nariño: Volcán de Cumbal, via Laguna Bolsa, 2740–2980 m, 11.ix.1944 (fl), *Ewan* 16139 (BM, S). Norte de Santandér: Ocaña to Pamplona, Serra Pl., 2400–3300 m, 30.viii.1878 (fl), *Kalbreyer* 711 (K), Putumayo: Lagunda de la Cocha, Quebrada de Santa Lucia, 2850 m, 8.i.1941 (fl), *Cuatrecasas* 11824 (COL, F). Risaralda: Municipio de Pereira, vicinity of La Laguna de Otún, 4000–4300 m, 3.ii.1980 (fl), *Díaz, Valencia & Jaromillo* 1738 (COL). Santandér: Páramo de Santurbán, Laguna de Cunta, 3880 m, 21.i.1927 (fl), *Killip & Smith* 17962 (COL, F). Tolima: Páramo de Ruíz, 3200–3500 m, 16–17.xii.1917 (fl), *Pennell* 2999 (F, K, MO). Valle: Río



Map 10 20. *H. laricifolium*: typical form ●, 'laricoides' ○; 21. *H. martense* ▲.

Bugalagrande, Barragán, Páramo de Bavaya, Corrales, 3550–3400 m, 10.iv.1946 (fl), *Cuatrecasas* 20569 (BM, F, P, U, US).

VENEZUELA. Lara: between Buenos Aires and Páramo de las Rosas, 2285–3290 m, 11.ii.1944 (fl), *Steyermark* 55501 (F). Mérida: Páramo de Mucuchies, x.1865 (fl), *Moritz* 1166 (BM, K, P, S); Sierra Nevada de Mérida, between La Cañada del Espejo and La Cañada de Los Anteojos, Torre de Befío, 4000–4130 m, 22.i.1973 (fl), *Cuatrecasas, Ruiz-Terán & López-Figueras* 28570 (BM, US); Páramo de Conejos, *c.* 8 km NE. of Mérida, 3800–4100 m, 27.xii.1967, *Wessels Boer* 2135 (NY, U, VEN). Táchira: Páramo de La Negra, 3000 m, 13.xi.1939 (fl), *Burrus & Müller* 1019a (VEN). Trujillo: El Paramito, Jagó to La Morita, hacia Tuñame, over 3000 m, viii.1958 (fl), *Aristeguiéta & Medina* 3488 (NY, VEN). Zulia: Zulia, 1983–1894 (fl), *Mocquerys* s.n. (NY, P).

ECUADOR. Azuay: 54 km from Cuenca on Suscal road, 3350 m, 13.ix.1969 (fl), *B. & C. Maguire* 61696 (BM, NY). Bolivar: Cordillera Occidental, Gualicon Loma, 3240 m, 7.x.1943, *Acosta Solís* 6263 (F). Cañar: Biblián to Cañar, north of Biblián, *c.* 3400 m, 23.iv.1968 (fl), *Harling, Storm & Ström* 8655 (GB, NY). Carchi: Páramo El Angel, between El Angel and Tulcán, 3450–3500 m, 14.v.1973 (fl), *Holm-Nielsen et al.* 5298 (AAU, F, S). Chimborazo: Cerro Chiguaza, *c.* 3200 m, 24.ix.1968 (fl), *Lugo* 475 (GB, NY). Cotopaxi: Cotopaxi, SW. slope, 3700 m, 3.vii.1939 (fl), *Asplund* 7516 (K, P, S). El Oro: NE. Zaruma, Tioloma, Hac. Ambocas, 3100 m, 30.viii.1947, *Espinosa* 2034 (NY). Imbabura: Cotacache to Apuela, 21 km (Intec valley), 3300 m, 11.viii.1976 (fl), *Øllgaard & Balslev* 8687 (AAU, BM, MO, U). Loja: 10 km south of Loja, 2800 m, 1–3.viii.1959 (fl), *Harling* 6239 (S). Napo: Cerro Antisana, Los Corrales, near Papallacta, 3900 m, 21.vii.1960 (fl), *Grubb et al.* 218 (K, NY). Pichincha: Mount Guamani, 3600–3800 m, 15.ix.1939 (fl), *Asplund* 8757 (K, P, S). Tungurahua: between Ambato and Baños, 10.i.1981 (fl), *D'Arcy* 13975 (BM, MO).

PERU. Amazonas: Chachapoyas, Cordillera Calla-Calla between Leimebamba and Balsas, 2900–3000 m, 21.x.1963 (fl & fr), *Ferreyra & Acleto* 15302 (MO, NY). Ancash: Cordillera Blanca, above Vicos, trail to Llacshacocha at Usacocha, 3350 m, 14.iii.1964 (fl), *Hutchinson & Wright* 4392 (F, K, MO, P, S). Cajamarca: 28 km N. of Cajamarca towards Pedernal, 12 km W. to Hacienda Granja Porcon (SIPA), 3260 m, 6.vi.1963 (fl), *D. & V. Ugent* 5463 (GH, K, WIS). Huánuco: Mito, *c.* 2700 m, 8–22.ii.1922 (fl & fr), *Macbride & Featherstone* 1610 (F, S). La Libertad: Huamacucho, Pullac to Parcay, 69 km, above Río Chuagón, 3920 m, 7.viii.1964 (fl), *Hutchinson, Wright & Straw* 6188 (F, K, MO). Piura: Huancabamba, distr. Sondor, 2300 m, 21.vii.1975 (fl), *Sagástegui, Cabanillas & Dias* 8214 (MO). San Martin: Huallaga, valley of Río Apisoncho 30 km above Jucusbamba, 3300 m, 5.viii.1965 (fl), *Hamilton & Holligan* 1090 (K, S).

H. laricifolium is closely related to *H. thuyoides*, and one collection from Cauca (*Fernández Pérez* 7159) is intermediate in some characters. Nearly always, however, *H. laricifolium* can be distinguished by the narrow rounded leaves with impressed midrib and straight margin.

H. laricifolium is very variable, but the variation appears to be continuous and not amenable to classification. From northern Ecuador and adjacent Colombia, where the leaves are relatively broad, there are clines north and south towards shorter, narrower, more densely imbricate leaves and smaller flowers with narrower, more acute sepals:

(i) North-eastward along the Cordillera Central to Venezuela; the extreme form from Boyacá north-eastward looks very different, with young shoots densely clothed with appressed leaves ('*H. laricoides*'). Both the typical form and '*H. laricoides*' occur in Boyacá and some parts of Cundinamarca, the latter favouring damper habitats. In other parts of Cundinamarca (e.g. Páramo de Guasca) and in Caldas, Risaralda, and Tolima, however, there is a continuous series of intermediate forms that does not allow the recognition even of subspecies.

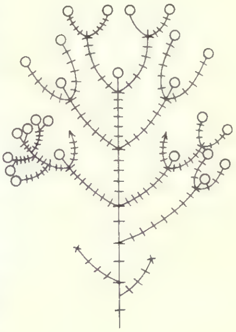
(ii) Southward through Ecuador to central Peru (Huánuco, Ancash) the leaves become gradually narrower and smaller, but not markedly imbricate, except for some populations from northern Peru.

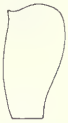
21. **Hypericum martense** N. Robson, **sp. nov.**

H. laricifolio Juss. affinis, sed habitu multo humiliori caespitosa, ramificationi praecipue pseudo-dichotomo, foliis valde punctatis, sepalis valde nervatis, petalis plerumque minoribus, staminibus paucioribus, stylis brevioribus, capsula angustiora, differt. Type: Colombia, Magdalena, Sierra Nevada de Santa Marta, near source of Río Yebosimeina, 3900 m, 25.v.1977 (fl), *Starker-White & Alverson* 586 (NY!, holotype; MO!, isotype!).

Icon: Fig. 8B.

Shrublet 0·08–0·16 m tall, forming clumps or cushions *c.* 15 mm in diam., with branches strict, mostly pseudo-dichotomous, or the outer decumbent but not rooting. *Stems* orange-brown, 4-lined and compressed when young, soon terete, cortex exfoliating irregularly; internodes 1–4 mm long. *Leaves* sessile, erect to closely imbricate, scarcely outcurving, not tetrastichous, persistent; lamina 4–7 × 0·6–0·8 mm, linear (upper) to acerose, incurved-canaliculate, cucullate, midrib not impressed, margin narrowly hyaline, concolorous, both surfaces dull, glaucous, subcoriaceous?; apex subacute to obtuse, base parallel, not clasping, pairs united to form very narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense, large, impressed beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 3–4 mm long, slender; upper leaves not transitional. *Flowers* 8–10 mm in diam., obconic (?). *Sepals* 4–5 × 0·8–1·3 mm, narrowly oblong, acute, incurved above; veins 5, unbranched, all prominent; glands mostly linear but striiform to punctiform near hyaline margin. *Petals* 6–8 × 2 mm *c.* 1·5 × sepals, oblong-obovate; apiculus acute; glands few, punctiform. *Stamens c.* 25, longest 4–5 mm long, *c.* 0·65 × petals. *Ovary c.* 1 × 0·5 mm, ellipsoid; styles 3, 2–2·5 mm long, *c.* 2–2·5 × ovary, outcurving to erect; stigmas broadly capitate. *Capsule* 4–5 × 2–2·5 mm, narrowly ellipsoid, obtuse, exceeding sepals. *Seeds* 1·2 mm long, ecarinate; testa finely scalariform-reticulate.





In rocky páramo, muddy places in high-rainfall areas; 3000–3900 m.

Colombia (Magdalena); confined to the Sierra de Santa Marta. Map 10 (p. 49).

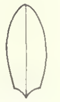
COLOMBIA. Magdalena: Sierra de Santa Marta, SE. slopes, Hoya del Río Donachuí, Meollaca, *c.* 3400 m, 8.x.1959, *Cuatrecasas & Romero Castañeda* 24644 (US); above San Miguel, *c.* 3000 m, vii.1932, *Seifriz* 421 (US).

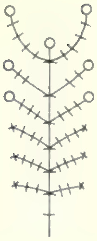
H. martense is a high-altitude derivative of the *'laricoides'* form of *H. laricifolium*. As a result of its dwarf, caespitose habit, however, the non-pseudo-dichotomous parts are much reduced, most of the clump being formed by pseudo-dichotomous (inflorescence) branching. The branches of a pseudo-dichotomy, however, usually bear lateral flowering branches.

22. **Hypericum hartwegii** Bentham

Pl. Hartwegiana: 127 (1843) [*'hartwegi'*]; Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 295 (1862) pro parte, quoad typum; R. Keller in Engler & Prantl, *Nat. Pflanzenfam.* **3** (6): 214 (1893), in *Bull. Herb. Boissier* II, **8**: 177 (1908), in Engler & Prantl, *op. cit.* 2nd ed. **21**: 181 (1925) pro parte, excl. pl. Colomb. Type: Ecuador, Loja, mountains near Loja, Chiquiribamba, vii.1841 (fl), *Hartweg* 721 (K!, holotype; BM!, K!, P!, W!, isotypes).

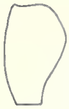
Shrub 0·3–0·9 m tall, erect, with branches strict to spreading, lateral, short (flowering) and long (extension) or rarely pseudo-dichotomous. *Stems* dark red-brown, 4-lined and ancipitous when young, eventually terete, without epidermal emergences, cortex exfoliating in strips; internodes 5–7 mm long. *Leaves* sessile, erect to ascending, closely imbricate, tetrastichous, persistent; lamina 5–7 × 2–3 mm, elliptic to oblong or obovate, plane, apically subconcave, not carinate but with midrib ± incrassate distally and subimpressed proximally beneath, margin narrowly hyaline, not glaucous, subcoriaceous; apex apiculate-obtuse to rounded, slightly cucullate, base cuneate to parallel, scarcely clasping, pairs united to form very narrow interfoliar ridge; basal vein 1, apparently unbranched; laminar glands quite





dense, not impressed or prominent, visible on both sides. *Inflorescence* 1-flowered, terminal and on short lateral branches; pedicel 1–2 mm long; upper leaves foliose. *Flowers* 15–20 mm in diam., stellate. *Sepals* 4–6 × 1·8–2·3 mm, ovate to oblong-elliptic, acute to subacute; veins *c.* 5, unbranched (?), midrib distally incrassate; glands linear. *Petals* bright (?) yellow, 8–11 × 4–5 mm, 2–2·5 × sepals, obovate; apiculus acute; glands striiform and punctiform. *Stamens* 45–50, longest 6–7 mm long, *c.* 0·5 × petals. *Ovary* 2–2·5 × *c.*1·4 mm, ovoid-ellipsoid; styles 3, 5–6 mm long, *c.* 2·5 × ovary, outcurving; stigmas small to subcapitate. *Capsule* and *seeds* not seen.

Habitat and phenology not recorded.

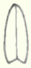


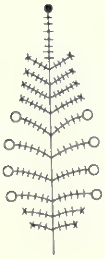
Ecuador (Loja). Known from only one collection. Map 9 (p. 46).
ECUADOR. Loja: see type.

H. hartwegii appears to be a very local relict species, being mostly closely related to *H. lycopodioides* (from east-central Colombia), which has spreading, incurved-conduplicate leaves with margin sometimes undulate, oblique-obovate petals, and more numerous stamens. See also 23 *H. maguirei*.

23. **Hypericum maguirei** N. Robson, **sp. nov.**

H. hartwegii Bentham affinis, sed foliis minoribus, dense imbricatis vaide cucullatis costa media subtus impressa, floribus minoribus, differt. Type: Ecuador, Azuay, 5km past San Miguel on road to Cuenca, 3350m, 15.x.1969 (fl), *B. & C. Maguire* 61707 (BM!, holotype; NY!, isotype).





Shrub 0·3–1 m tall, erect or spreading; branches strict or ascending, lateral, short (flowering) and long (extension), narrowly spiciform to pyramidal, sometimes secund. *Stems* dark red-brown, 4–6 lined when young, eventually terete, without epidermal emergences, cortex exfoliating in strips or irregular flakes; internodes 1–3 mm, long. *Leaves* sessile, suberect to erect, ± densely imbricate, tetrastichous, persistent; lamina 2–4 × 0·4–1·2 mm, ± narrowly oblong to narrowly elliptic or linear, incurved, midrib impressed beneath, pale lucent green with margin narrowly hyaline and plane, not glaucous, coriaceous; apex obtuse to rounded, markedly cucullate, base narrowly cuneate to parallel-sided, not or scarcely clasping, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense or in one row beneath, not impressed or prominent, sparser above. *Inflorescence* 1-flowered, terminal and on short lateral branches; pedicel 1–3 mm long; upper leaves foliose. *Flowers* (5–)8–15 mm in diam., stellate (to obconic ?). *Sepals* 2–5 × 0·7–7·1 mm, acute, incurved-cucullate, margin hyaline; veins 3–5, unbranched, midrib prominent beneath; glands linear, distally punctiform. *Petals* golden to orange-yellow, 3–8 × 1·5–4 mm, 1·5–2 × sepals, obovate to oblong-obovate; apiculus subacute to obsolete; glands striiform and punctiform. *Stamens* 25–40, longest 2–6 mm long, 0·6–0·75 × petals. *Ovary* 1–2 × 0·5–1·2 mm, narrowly ovoid to ellipsoid; styles 3, 2–5 mm long, 1·5–2·5 × ovary, spreading-incurved; stigmas small. *Capsule c.* 3 × 2 mm, narrowly ovoid-ellipsoid, equalling sepals. *Seeds* not seen.

On dry slopes with mostly low shrubs and ferns, and drier grassland; 2400–3350 m.

Southern Ecuador (Azuay, Loja, El Oro). Map 9 (p. 46).
ECUADOR. Azuay: Cuenca to Oña, Hacienda Pizhia, *c.* 2800 m, 23.ix.1955 (fl), *Asplund* 17766 (S). Azuay/Loja: Nudo del Cordillera Occidental y Cordillera Oriental entre Oña y Rancho Ovejero, 2704–2800 m, 1–2.viii.1959 (fl), *Barclay & Juajibioy* 8452 (NY). El Oro: between Curtincapa and Guagra Uma, 13 km NE. of Curtincapa, 2850 m, 16.viii.1943 (fl), *Steyermark* 53912 (F). Loja: about Oña, 2400 m, n.d. (fl), *Jameson* s.n. (K).

Larger specimens of *H. maguirei* at first sight resemble a small version of *H. lycopodioides*, but differ from it in the sessile, markedly cucullate, imbricate leaves with midrib impressed beneath, as well as in size of parts. It is most closely related to *H. hartwegii*, which has larger, almost plane leaves and larger flowers. Although these two populations are very close in distribution, they are morphologically so distinct that they should be treated as separate species.

24. **Hypericum magniflorum** Cuatrec.

in *Ciencia, Mex.* **4**: 64, f. 1. (1943); Steyermark in *Fieldiana Bot.* **28**: 988 (1967). Type: Colombia, Norte de Santandér, Cordillera Oriental, Páramo de Tamá, near La Cueva, 27.x.1941 (fl), *Cuatrecasas, Schultes & Smith* 12634 (COL, holotype; F!, GH!, P!, U!, isotypes).

Icon: Fig. 9.

Shrub 1–2·5 m tall, erect, with branches strict, mostly pseudo-dichotomous, sometimes lateral. *Stems* yellow-brown, 4-lined when young, without epidermal emergences, soon terete, cortex flaking irregularly; internodes 2–3 mm long. *Leaves* sessile, spreading abruptly from above base, ± tetrastichous, becoming brown but

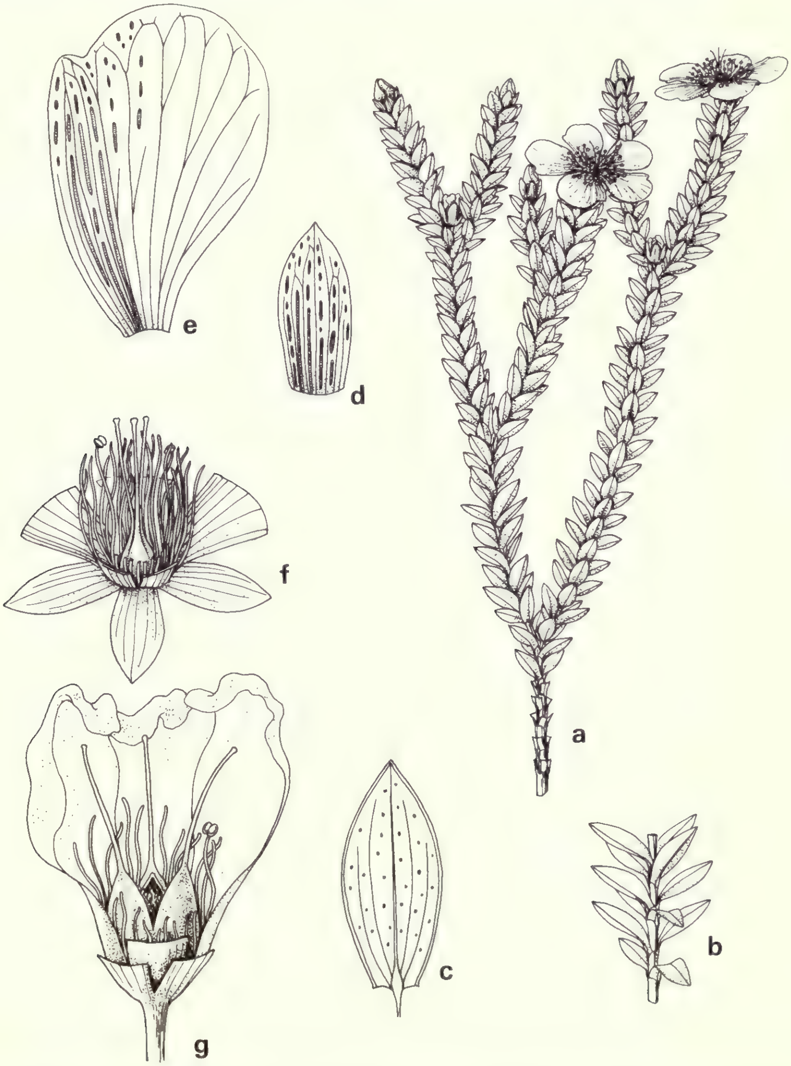
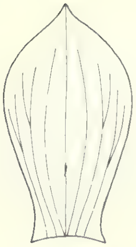
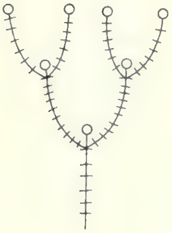
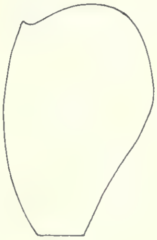


Fig. 9 *H. magniflorum*: (a) habit; (b) stem with leaves; (c) leaf; (d) sepal; (e) petals; (f) stamens (partly cut away) and ovary; (g) capsule (a, b × ½; c–g × 2). (b) *Cuatrecasas & Rodriguez* 27789; others *Steyermark* 57378.





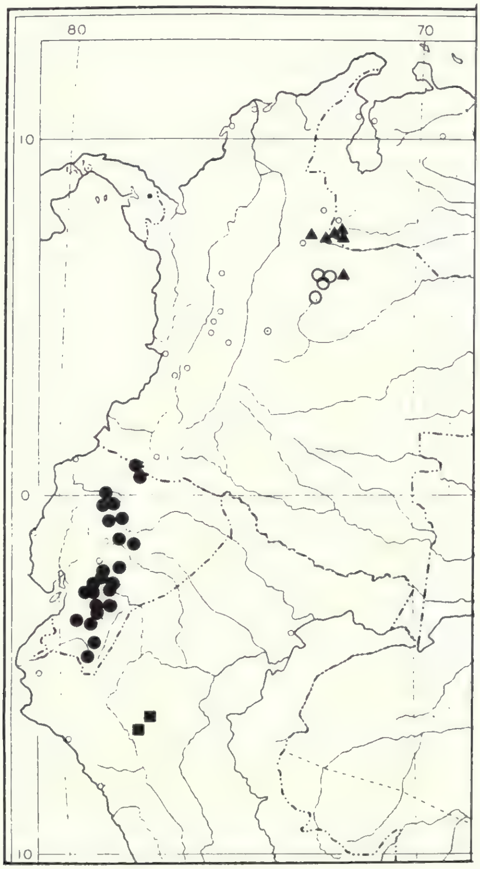


not deflexed, persistent until cortex is shed; lamina 10–18 × 4–8 mm, elliptic to oblanceolate-spathulate, plane, slightly cucullate, carinate, concolorous or paler beneath, not glaucous, chartaceous; apex acute to obtuse-apiculate, base angustate, sheathing, pairs united to form very narrow interfoliar ridge; basal veins 5–7, parallel or almost so, branching distally, with tertiary reticulation sometimes visible beneath; laminar glands dense above, sparse or absent beneath, slightly prominent. *Inflorescence* 1-flowered, sometimes with several short flowering branches crowded together, usually with pseudo-dichotomous branches from 1st or 2nd node below; pedicel up to 5 mm long; upper leaves transitional. *Flowers c.* 35 mm in diam., stellate. *Sepals* 9–11 × 3·5–5 mm, broadly oblong to obovate-spathulate, acute to obtuse; veins 11–19, dichotomising distally, with midrib scarcely prominent beneath; glands punctiform in upper third. *Petals* rich yellow, 16–22 × 12–14 mm, *c.* 2 × sepals, obovate-oblanceolate; apiculus acute; glands punctiform distally. *Stamens c.* 80, longest 9–11 mm long, *c.* 0·5 × petals. *Ovary* 4–5 × 2–3 mm, broadly ellipsoid to subglobose; styles 3, 5–9 mm long, 1·5–2 × ovary, erect, free, outcurved below apex; stigmas slightly enlarged to broadly capitate. *Capsule c.* 7 × 5 mm, broadly ellipsoid, shorter than sepals. *Seeds* not seen.

On rocky slopes of limestone outcrops; 3000–3800 m.

Eastern Colombia (Boyacá, Santandér, Norte de Santandér) and adjacent Venezuela (Táchira). Map 11.

COLOMBIA. Boyacá: Páramo de Chitá, cabeceras de Río Casanare, 3080 m, 19.vi.1972 (fl), *Cleef* 4743 (BM, U). Norte de Santandér (see also type): Bucaramanga, Cumbre of Páramo Mortiño, Cucuta road, 3300 m, v.1948 (fl), *Sandeman* 6077



Map 11 24. *H. magniflorum* ▲; 27. *H. stuebelii* ■; 30. *H. decandrum* ●; 61. *H. cymobrathys* ○.

(K). Santandér: Páramo de Santurbán, *c.* 3000 m, 27.viii.1948 (fl & fr), *Barkley & Araque* 18S155 (F, COL).

VENEZUELA. Táchira: Páramo de Tamá, near Colombo-Venezuelan boundary, 3045–3475 m, 15.vii.1944 (fl). *Steyermark* 57378 (F, NY); NNE. slopes of Pata de Judío, 2500–3100 m, 19.x.1978 (fl & fr), *Luteyn* 5945 (BM, VEN).

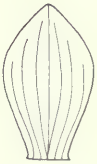
Though clearly related to *H. terrae-firmae, H. magniflorum* is constantly 3-styled. The abrupt outward bend of the leaves is characteristic, as is the persistent leaf with a sheathing narrowed base.

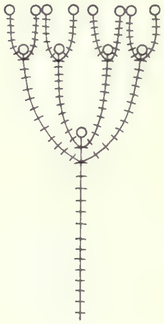
25. **Hypericum gleasonii** N. Robson, **sp. nov.**

H. magnifloro Cuatrec. affinis, sed foliis brevioribus, plusminusve imbricatis, interdum viscidis, supra basin deciduis, stylis brevioribus stigmatibus manifeste capitatis, differt. Type: Colombia, Santandér, Páramo de Almorzadero, *c.* 32–34 km S. of Chitagá, *c.* 3400 m, 12.v.1979 (fl), *Luteyn* 7653 (COL!, holotype; BM!, NY!, isotypes).

H. platyphyllum Gleason in *Bull. Torrey bot. Club* **56**: 106. (1929) pro parte, quoad *Killip & Smith* 15616 pro parte.

Shrub 0·15–1·5 m tall, erect, with branches strict, mostly pseudo-dichotomous, sometimes lateral. *Stems* yellow-brown, 4-lined when young, eventually terete, without epidermal emergences, cortex flaking irregularly; internodes 2–3 mm long. *Leaves* sessile, outcurved-ascending to imbricate-erect, tetrastichous, deciduous above base before fading; lamina 7–10 × 3–6 mm, oblanceolate to obovate, incurved, not cucullate or carinate, concolorous, not glaucous, subcoriaceous to coriaceous; apex acute or apiculate to obtuse, base angustate, sheathing, pairs united (at least when young) to form narrow interfoliar ridge; basal veins 5–7, flabellate, branching distally (sometimes obscurely), reticulation obscure beneath; laminar glands dense, not or slightly prominent, visible beneath; marginal glands usually secreting viscous clear or white resin. *Inflorescence* 1-flowered usually with pseudo-dichotomous branches from 1st to 3rd node below and often with 1 or 2 lateral branches immediately below these, forming flower cluster when young; pedicel 3–6 mm long; upper leaves transitional. *Flowers* 20–40 mm in diam., stellate. *Sepals* 6–10 × 3–5 mm, elliptic to oblanceolate, acute to apiculate or obtuse; veins 9–15, sometimes dichotomising distally, with midrib scarcely prominent beneath; glands punctiform in upper third to two-thirds. *Petals* rich yellow, (always?) tinged red beneath, 12–20 × 10–11 mm, *c.* 2 × sepals, oblanceolate to obovate; apiculus obtuse to rounded; glands distally punctiform. *Stamens* 80–100, longest 6–10 mm long, *c.* 0·5 × petals. *Ovary* 3–4 × 2–3 mm, broadly ellipsoid to ovoid; styles 3, 4–6 mm long, 1·25–1·5 × ovary, free, suberect to spreading; stigmas broadly capitate. *Capsule* 5–6 × 5–6 mm, subglobose, shorter than sepals. *Seeds* not seen.

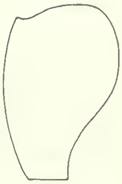




In open páramo on fine talus or grassy slopes; 3200–3900 m.

Colombia (Norte de Santandér, Santandér). Apparently confined to the Páramo del Almorzadero. Map 9 (p. 46).

COLOMBIA. Norte de Santandér: Valley of río Chitagá, 20 km SE. of Chitagá, 3475 m, 24.ix.1944 (fl & fr), *St. John* 207784 (COL, NY). Santandér: Páramo del Almorzadero, 3600–3800 m, 28.xi.1941 (fl), *Cuatrecasas* 13495 (COL, GH, NY, P); Páramo del Almorzadero, between Chitagá and Cerrito, 3900 m, 31.xii.1959–1.i.1960 (fl), *Barclay & Juajibioy* 10389 (NY); Peralonso, Platera, 3400 m, 20.ix.1969 (fl), *Cuatrecasas & Rodriguez* 27828 (BM, COL, US); Peralonso, 3200 m, 19.vii.1940 (fr), *Cuatrecasas & Garcia Barriga* 9887 (COL).



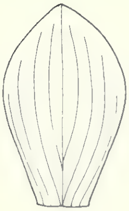
H. gleasonii is a relict species intermediate between *H. magniflorum* and *H. mexicanum*. It has larger flowers than *H. mexicanum*, and these are solitary, but it shares with that species the deciduous leaves with viscous secretions. In *H. gleasonii* the leaves are smaller than those of *H. mexicanum* (from Cundinamarca and Boyacá) but with a comparable erect habit; the form of *H. mexicanum* that grows in the same area is a small-flowered shrublet with decumbent rooting stems.

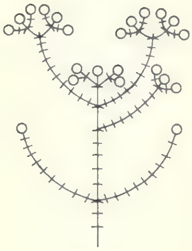
Killip & Smith 15616 (from the Páramo de Las Vegas), which Gleason (1929) placed in *H. platyphyllum*, is a puzzling collection. The BM and COL specimens belong to *H. mexicanum*, but the NY specimen has larger flowers and tends towards *H. gleasonii*.

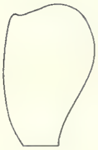
26. **Hypericum mexicanum** L.

Diss. Hyperic.: 5, f. 2 (1776), *Amoen. Acad.* **8**: 322, t.8, f.2 (1785); L. fil., *Suppl. Pl.*: 345 (1781); Lam., *Encyl. méth.* (Bot.) **4**: 169 (1797); Gleason in *Bull. Torrey bot. Club* **56**: 103 (1929). Type: Colombia [Cundinamarca], *Mutis* in Herb. Linn. 943: 31 (LINN!, holotype; BM!, isotype).

Hypericum ? mexicanum sensu Choisy, *Prodr. monogr. fam. Hypéric.*: 60 (1821).
Hypericum mutisianum Kunth in Humboldt, Bonpland & Kunth, *Nov. Gen. et Sp. Pl.* **5**: 185 (1822), nom. illegit.; R. Keller in *Bull. Herb. Boissier* II, **8**: 178 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Knuth in *Reprium Sp. nov. Regni veg.*, Beih. **43**: 483 (1927). Type: Colombia, Cundinamarca, near Santa Fé de Bogota, 2457 m, 1805 (fl), *Humboldt & Bonpland* s.n. (P-HUM!, holotype; B-WILLD, isotype);
Brathys mutisiana (Kunth) Spach, *Hist. nat. vég.* Phan. **5**: 447 (1836); in *Annls Sci. nat.* (Bot.) II, **5**: 366 (1836).
Hypericum resinosum Bentham, *Pl. Hartweg.*: 165 (1845); R. Keller in *Bull. Herb. Boissier* II, **8**: 177 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925). Type: Colombia. Cundinamarca, 1841–1843 (fl), *Hartweg* 924 (K!, holotype; BM!, P!, W!, isotypes).
H. mexicanum var. *intermedium* Kuntze, *Rev. Gen. pl.* **1**: 59 (1891). Type: Venezuela, Mérida, Silla de Caracas, *Kuntze* s.n. (NY, holotype).





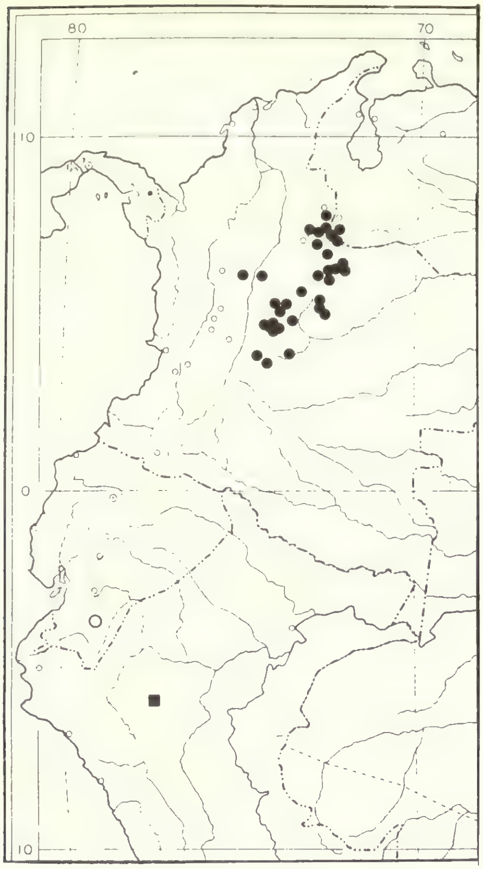


Shrub or shrublet 0·15–1·5(–2) m tall, erect or decumbent and sometimes rooting at the base, with branches strict, pseudo-dichotomous and sometimes lateral especially from short upper internodes. *Stems* yellow- to orange-brown, 4-lined when young, eventually terete, cortex flaking irregularly; internodes 2–8 mm long. *Leaves* sessile, outcurving-ascending to imbricate-erect, tetrastichous, deciduous above base usually without withering; lamina 7–17 × 3–10 mm, elliptic or oblanceolate to obovate, plane to subconduplicate, not or scarcely cucullate, not carinate, concolorous, not glaucous, coriaceous; apex obtuse or rounded, base cuneate to angustate, ± sheathing, pairs united to form narrow interfoliar ridge; basal veins 5–7, flabellate, branching and anastomosing distally, reticulation clearly to obscurely visible beneath; laminar glands dense to sparse, usually visible and sometimes slightly prominent beneath; marginal glands secreting viscous clear or white resin. *Inflorescence* 1–5(–13)-flowered, cymose, corymbose, often with 1–3 pairs of pseudo-dichotomous branches from 1–3 nodes close below; peduncle and pedicels 1–6 mm long; upper leaves transitional. *Flowers* 15–25 mm in diam., stellate. *Sepals* 5–9 × 2–4 mm, elliptic to oblanceolate-spathulate or obovate, acute to apiculate or obtuse; veins 5–9, sometimes dichotomising distally, with midrib scarcely prominent beneath; glands punctiform distally. *Petals* golden yellow, (always?) tinged red beneath, 9–12 × 4–9 mm, 1·3–2 × sepals, obovate-oblanceolate to obovate-oblong; apiculus obtuse to obsolete; glands punctiform distally. *Stamens c.* 50, longest 5–7 mm long, *c.* 0·5 × petals. *Ovary* 2·5–3 × 1·8–2 mm, broadly ellipsoid to ovoid; styles 3, 2·5–4 mm long, 1–1·2 × ovary, suberect; stigmas broadly capitate. *Capsule* 5–7 × 4–6 mm, broadly ellipsoid to subglobose, equalling or exceeding sepals. *Seeds c.* 0·7 mm long, ecarinate; testa finely scalariform.

In open páramo on fine talus or grassy slopes or in scrub; (1700)2400–4200 m.

Western Venezuela (Mérida, Táchira) and north-eastern to central Colombia (Norte de Santandér to Valle de Cauca). Map 12.

COLOMBIA. Antioquía: entre Río Negro y Sta Helena, 20650 m, vii.1944 (fl), *Garcia Barriga*. 11094 (COL). Boyacá: Sierra Nevada del Cocuy, Quebrada de San



Map 12 26. *H. mexicanum* ●; 28. *H. prietoi* ○; 29. *H. cassiopiforme* ■.

Paulino proximo Alto Ritacuva, *c.* 3650, 3.v.1959 (fl), *Barclay & Juajibioy* 7525 (COL, MO, NY); Páramo de Güina, 3200 m, 17.vii.1940 (fl), *Cuatrecasas & Garcia Barriga.* 9783 (COL). Cundinamarca: Páramo de Guasca, 2840 m, 15.xii.1938 (fl), *Balls* 5700 (BM, COL, K); Sabana de Bogotá, Municipio de Tenjo, Vereda de la Punta, 2800–2670 m, 29.i.1966 (fl & fr), *Cuatrecasas & Jaramillo* 26755 (BM, COL, US); Cerro de Monserrate, 3000 m, 10.iii.1966 (fl), *Duque-Jaramillo* 2877 (COL). Meta: Macizo de Sumapaz, alredores de la Laguna La Guitarra, 3370–3400 m, 5.vii.1981, *Díaz P.* 2485 (COL). Norte de Santandér: Páramo de Fontibón, 2700 m, 27.vii.1940 (fl), *Cuatrecasas & Garcia Barriga.* 10088 (NY, US). Santandér: Páramo de Santurbán, 3600 m, 27.viii.1948 (fl), *Araque & Barkley* 18s004 (COL, F). Valle: Rio Cali, Pichinde, 1700 m, vii.1938 (fl), *Duque-Jaramillo* 4107 (COL).

VENEZUELA. Mérida: Silla de Caracas, *Kuntze* s.n. (NY). Táchira: Páramo de Tamá, 4000 m, 1937 (fl), *Cardona* 123 (US, VEN).

H. mexicanum is a misnomer, as the type comes from Cundinamarca and the species as a whole is confined to Colombia and adjacent Venezuela. In attributing Mutis collections to Mexico, Linnaeus made the same mistake here as he did in the case of *Vismia baccifera*.

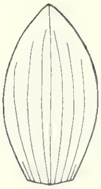
H. mexicanum differs from *H. gleasonii* in having larger, more spreading leaves and smaller flowers, which are frequently in condensed cymes. The two species remain distinct where their distributions overlap in the Páramo del Almorzadero.

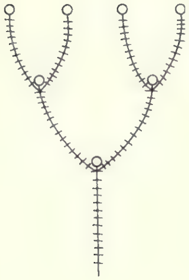
Gleason (1929) confused the eastern form of *H. mexicanum* with *H. platyphyllum*, which has penninerved (not flabellate-nerved) leaves and smaller stigmas and is treated here as a subspecies of *H. phellos*.

27. **Hypericum stuebelii** Hieron.

in *Bot. Jahrb.* **21**: 321 (1895); R. Keller in *Bull. Herb. Boissier* II, **8**: 177 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925) Type: Peru, Amazonas, Chachapoyas, between Pacasmayo and Moyobamba, near Mojon Cruz, 3300 m, iv.–vi.1875? (fl), *Stübel* Peru 27 (B†; holotype; F!, GH!, NY!, photographs).

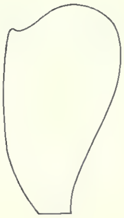
Hypericum stuebelii Hieron. ex R. Keller in *Bot. Jahrb.* **42**: 129 (1908). Type: as for *H. stuebelii* Hieron.





Shrub 0·3–1 m tall, erect, with branches strict or ascending, pseudo-dichotomous. *Stems* reddish-brown, 4-lined when young, soon terete, cortex exfoliating in irregular flakes; internode 3–4 mm long. *Leaves* sessile, closely imbricate and tetrastichous at first, gradually outcurving, deciduous above the base usually before fading; lamina 8–14 × 3–7 mm, broadly elliptic-ovate to elliptic-lanceolate, incurved-cucullate, midrib prominent distally beneath, margin scarcely distinct, concolorous, yellow-green, not glaucous, coriaceous; apex obtuse or apiculate to acute, base angustate, sheathing, pairs united to form rather deep (0·4–1 mm) interfoliar ridge; basal or near-basal veins 7–9, flabellate, not clearly branched, tertiary reticulum not visible; laminar glands dense, not prominent, visible above and sometimes beneath. *Inflorescence* 1-flowered, usually with pseudo-dichotomous branches from node below; pedicel 4–6 mm long; upper leaves not transitional. *Flowers* 25–40 mm in diam., stellate. *Sepals* 10–12 × (2–)3–6 mm, elliptic-ovate to lanceolate, obtuse to acute, cucullate; veins 7–11, sometimes dichotomising distally, prominent beneath; glands linear, punctiform in distal third. *Petals* bright? yellow, 15–20 × 5–10 mm, 1·5–1·7 × sepals, obovate; apiculus subacute to obtuse; glands linear, interrupted distally. *Stamens* 80–150, longest 7–10 mm long, *c.* 0·5 × petals. *Ovary c.* 4·5–5 × 2·5 mm, ellipsoid; styles 3–4, *c.* 7 mm long, *c.* 1·7 × ovary, free, suberect to outcurved; stigmas not or scarcely enlarged. *Capsule c.* 7–8 × 5 mm, broadly ellipsoid to subglobose, shorter than sepals. *Seeds* not seen.

On open hillsides, (always ?) in damp or wet areas; 2400–3300 m.



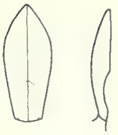
Northern Peru (Amazonas, San Martin), almost confined to a small region round Chachapoyas. Map 11 (p. 54).

PERU. Amazonas: Chachapoyas, 1–5 km W. of Molinopampa, Jalca zone, 2400–2450 m, 18.vii.1962 (fl), *Wurdack* 1353 (F, GH, K, NY, P, S, US); La Jalca near Chachapoyas, 2700–3300 m, i.1930 (fl), *Williams* 7585 (F, NY); Chachapoyas, Pass of Piscohuañuna, 2700 m, viii.1938 (fl), *Sandeman* s.n. (K); Cordillera of Piscohuañuna between Chachapoyas and Moyobamba, xii.1868 (fl), *Raimondi* 2096 (NY). San Martin: Bagazan, 1835 (fl), *Mathews* 1609 (K).

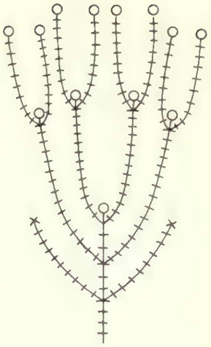
H. stuebelii appears to be a relict species with no ancestral relatives nearer than NE. Colombia (*H. magniflorum, H. pimeleoides*). Its leaves vary from broad, obtuse, and almost plane to narrow, acute, and incurved.

28. **Hypericum prietoi** N. Robson, **sp. nov.**

H. stuebelii Hieron. affinis, sed ramis strictioribus, foliis minoribus densissimis manifeste quadrifariis, 1-nervis, parte distali obtuse carinata parte proximali subtus costa media impressa, floribus minoribus, differt. Type: Ecuador, Azuay, Eastern Cordillera, between Oña and the río Yacuambi, 3000–3360 m, 10–19.ix.1945 (fr), *Prieto* P-302 (NY!, holotype).



Shrub c. 0·3 m tall, erect; branches very strict, pseudo-dichotomous and lateral. *Stems* reddish-brown, 4–6-lined when young, eventually terete, cortex exfoliating in irregular flakes; internodes *c.* 2 mm long. *Leaves* sessile, very closely imbricate, markedly tetrastichous, laterally compressed distally, not becoming outcurved, deciduous above the base before fading; lamina 7–8 × 1·5–2 mm, oblanceolate, distally obtusely carinate and cucullate, midrib impressed proximally beneath, margin very narrowly hyaline, concolorous, lustrous yellow-green, not glaucous, coriaceous; apex acute, base parallel-sided, scarcely sheathing, pairs united to form shallow to rather deep (to 1·5 mm) interfoliar ridge; basal vein 1, unbranched;



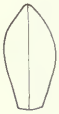
laminar glands dense, not visible beneath. *Inflorescence* 1-flowered, with pseudodichotomous branches from node below; pedicel 2–2·5 mm long; upper leaves not transitional. *Flowers* stellate? *Sepals* 7–8 × 2 mm, lanceolate, acuminate, compressed-cucullate; veins 3–5, unbranched, prominent beneath; glands linear. *Petals* and *stamens* not seen. *Ovary* with styles 3, *c.* 4 mm long, suberect; stigma narrowly capitate. *Capsule* 5 × 2·5 mm, broadly ellipsoid, shorter than sepals. *Seeds* 1·2 mm long, ecarinate; testa finely scalariform.

On the crest of the Cordillera; 3000–3360 m.

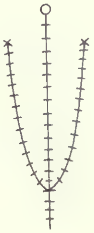
Ecuador (Azuay). Map 12 (p. 57).
ECUADOR. Azuay: Eastern Cordillera between Oña and the río Yacuambi, 3000–3360 m, 10–19.ix.1945 (fr), *Prieto* P-302 (NY).

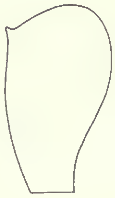
H. prietoi, which has been collected once only, resembles *H. stuebelii* but has smaller, laterally compressed, and markedly tetrastichous leaves and stricter branches, some of which are lateral.

29. **Hypericum cassiopiforme** N. Robson, **sp. nov.**



H. stuebelii Hieron. affinis, sed ramis basalibus lateralibusque strictioribus, foliis minoribus, oblanceolatis vel obovato-oblanceolatis, floribus minoribus, staminis paucioribus, stylis brevioribus, differt. Type: Peru, Amazonas, Chachapoyas, 1–5 km W. of Molinopampa, 2400–2450 m, 18.vii.1962 (fl), *Wurdack* 1355 (US!, holotype).





Shrub c. 0·3 m tall, erect, with branches strict, basal and lateral. *Stems* reddish-brown, 4-lined when young, eventually terete, cortex exfoliating in irregular flakes; internodes 2–4 mm long. *Leaves* sessile, imbricate-tetrastichous but not usually laterally compressed distally, becoming outcurved, deciduous above the base before fading; lamina 7–8 × 2·5–3 mm, oblanceolate, incurved-cucullate but scarcely carinate, midrib slightly prominent to scarcely impressed beneath, margin narrowly, hyaline otherwise concolorous, lustrous yellowish-green, not glaucous, subcoriaceous; apex subacute, base cuneate, broadening below, scarcely sheathing, pairs united to form narrow interfoliar ridge; basal vein 1 with 2 obscure near-basal branches; laminar glands dense, more visible above than beneath. *Inflorescence* 1-flowered; pedicel *c.* 3·5 mm long; upper leaves not transitional. *Flowers c.* 25 mm in diam., stellate. *Sepals* 8 × 1·8–2·3 mm, elliptic to oblong, acute, incurved-cucullate, reddish; veins 5, unbranched, prominent beneath; glands linear, distally punctiform. *Petals* bright yellow tinged red, *c.* 14 × 9 mm, *c.* 1·7 × sepals, obovate-oblanceolate; apiculus acute; glands linear. *Stamens c.* 50, longest *c.* 10–11 mm long, *c.* 0·5 × petals. *Ovary c.* 4 × 1·7 mm, ellipsoid; styles 3, *c.* 5 mm long, *c.* 1·2 × ovary, suberect ?; stigmas narrow. *Capsule* and *seeds* not seen.

In the *Jalca* zone; 2400–2450 m.

Peru (Amazonas). Map 12 (p. 57).
PERU. Amazonas: 1–5 km W. of Molinopampa, 2400–2450 m, 18.vii.1962 (fl), *Wurdack* 1355 (US).

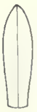
H. cassiopiforme, like *H. prietoi*, is based on a single collection and appears to be related directly to *H. stuebelii*. It is smaller, with smaller leaves and flowers and more slender stems, and is intermediate in form between *H. stuebelii* and *H. decandrum*. It differs from the latter by the broader leaves, the larger flowers with broader sepals and the longer styles with narrow stigmas.

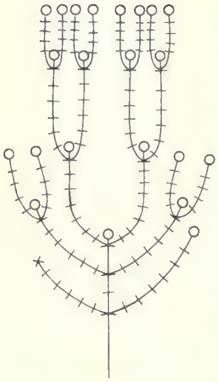
30. **Hypericum decandrum** Turcz.

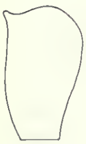
in *Bull. Soc. Nat. Moscou* **31** (1): 389 (1858). Type: Ecuador [Pichincha (?)], Quito, [1865?] (fl), *Jameson* 62 (LE, holotype; BM!, K!, W!, isotypes).

Hypericum gnidioides var. *polytrichoides* R. Keller in *Bull. Herb. Boissier* II, **8**: 183 (1908). Type: Ecuador, Chimborazo, in pascuis montis Titaicún, 3900 m, xi.1859 (fr), *Spruce* 5599 (G!, holotype, F!, photograph; BM!, C!, GH!, K!, NY!, P!, W!, isotypes).

Icon: Fig. 10.







Shrub or shrublet (or perennial herb?) 0·1–0·6 m tall, erect or decumbent and rooting with branches strict, basal (from decumbent and rooting portion) and pseudo-dichotomous or sometimes lateral. *Stems* reddish- to yellowish-brown, 4–6-lined when young, soon 2-lined, eventually terete, cortex exfoliating in irregular flakes; internodes 1–5 mm long. *Leaves* sessile, erect and subimbricate to narrowly spreading or slightly outcurving, deciduous above the base before fading; lamina 4–15 × 0·7–3 mm, ± narrowly oblanceolate to narrowly oblong, ± incurved-cucullate, midrib distally prominent otherwise impressed or plane beneath, concolorous or with margin rather narrowly hyaline, lustrous pale green, not glaucous, subcoriaceous; apex acute, base angustate, broadening below, not or scarcely sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched or with 1–2 pairs of obscure lateral branches; laminar glands dense, visible above only, or obscure. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 2·5–7 mm long; upper leaves not transitional. *Flowers* 6–20 mm in diam., stellate. *Sepals* 3·5–9 × 1–3 mm, narrowly elliptic to narrowly oblong, acute, compressed-cucullate, green (not reddish); veins 5–7, unbranched, sometimes becoming prominent; glands linear, punctiform in distal third to half. *Petals* bright yellow tinged red (? always), 5–9 × 2–3 mm, 0·9–1·2 × sepals, obovate-oblong to oblanceolate-oblong; apiculus acute; glands absent. *Stamens* (5)10–45, longest 2·5–4 mm long, *c.* 0·5 × petals. *Ovary* 2·5–3 × 1–1·5 mm, ellipsoid; styles 3(4), 1·5–3 mm long, *c.* 0·5–1 × ovary, divergent; stigma narrowly to broadly capitate. *Capsule* 3·5–5 × 2–3 mm, ellipsoid to cylindric-ellipsoid, shorter than sepals. *Seeds* 0·7–0·8 mm long, ecarinate; testa finely scalariform.

In grassy or shrubby slopes of the páramo and subpáramo; (2200 ?) 2700–3930 m.

Ecuador (in scattered localities from Carchi to Loja), Peru (Amazonas). Map 11 (p. 54).

ECUADOR. Azuay: Loja to Cuenca, between Km 113 and 124, 2700–3000 m, 26.ix.1969 (fl & fr), *B. & C. Maguire* 44320 (BM, NY). Cañar: Rivera NE. of Pindilig, 2900 m, 13.xii.1980 (fl & fr), *Holm-Nielsen, Jaramillo & Coello* 29222 (AAU). Carchi: Nudo de Boliche, Voladero, 3800 m, 12.vi.1939 (fl & fr), *Penland* 900 (F, GH, NY). Chimborazo: Mt. Titaicún, 3900 m, xi.1858 (fl), *Spruce* 5599 (BM, C, GH, K, NY, P, W). Loja: N. of Saraguro, 3045 m, 4.viii.1943 (fr), *Steyermark* 53743 (F, NY). Morona-Santiago: Páramo de Hatanga, Km 36 on road Sigsig-Gualaquiza, E. of pass, 3300 m, 14.xii.1980 (fl), *Holm-Nielsen, Jaramillo & Coello* 29386 (AAU). Napo: Valle de Chalupas near junction of Río Chalupas and Río Aguas Buenas, 3200 m, 20.i.1980 (fl), *Holm-Nielsen* 21014 (AAU). Pichincha?: Quito, 1865? (fl), *Jameson* 62 (BM, K, W). Tungurahua: Cordillera de Llanganates, near junction of río Golpe and río Sangarinas (Desaguadero), 26.xi.1939 (fl & fr), *Asplund* 9989 (S).

PERU. Amazonas: Cerro San Marino, Amaybamba, 3100 m, iii.1919 (fr), *Bues* 567 (US).

H. decandrum is most frequent towards the south of Ecuador and absent or rare in some central parts of that country. It is related to *H. cassiopiforme* but differs in the longer, often narrower, less closely imbricate leaves and the smaller flowers with shorter, capitate styles. It is quite variable, the most reduced, weaker-stemmed form from the extreme south of its range being considerably different from the sturdy northern plants.

31. **Hypericum pimeleoides** Planchon & Linden ex Triana & Planchon

in *Annls Sci. nat.* (Bot.) IV, **18**: 299 (1862); Gleason in *Bull. Torrey bot. Club* **56**: 103 (1929). Type: Colombia, Norte de Santandér, Prov. de Ocaña, Cerro Pelado, 2270 m, ii.1846–1852 (fl), *Schlim* 443 (sphalm. 243) (COL?, holotype; BM!, K!, KW!, P!, US!, isotypes).

Hypericum caracasanum var. *ocanense* R. Keller in *Bull. Herb. Boissier* II, **8**: 183 (1908). Type: as for *H. pimeleoides* (G!, holotype).

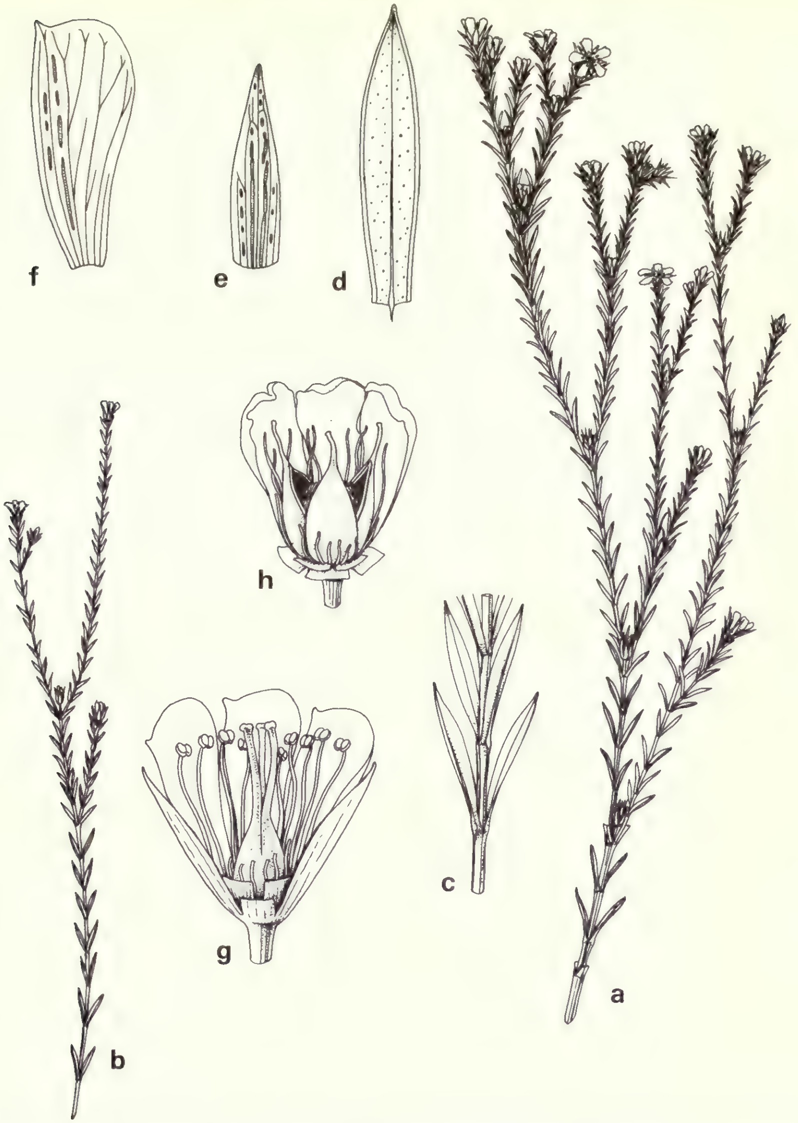
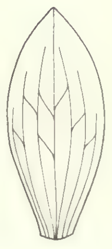
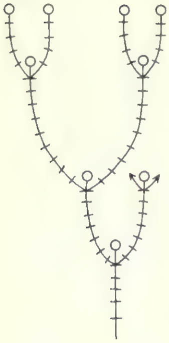


Fig. 10 *H. decandrum*: (a) habit, large form; (b) habit, small form; (c) stem with leaves; (d) leaf; (e) sepal; (f) petal; (g) stamens (partly cut away) and ovary; (h) capsule (a, b × ½; c–h × 5). (b) *Espinosa* 923; others *B. & C. Maguire* 61708.

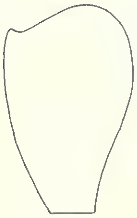
Shrub 0·4–1·5 m tall, erect, with branches strict, pseudo-dichotomous and occasionally lateral. *Stems* yellow- to orange-brown, 4-lined and compressed when young, the subfoliar ridge broad, soon terete, cortex exfoliating in strips; internodes 3–6 mm long. *Leaves* sessile or with broad petiole to 1·5(–2) mm long, densely imbricate and scarcely outcurving to laxly imbricate and narrowly spreading, ± markedly tetrastichous, deciduous above petiole without fading; lamina 10–24 × 3·5–10·5 mm, broadly to narrowly elliptic, plane, not or scarcely cucullate, midrib not prominent beneath, margin not distinct or rarely indurated, concolorous, glaucous, coriaceous; apex acute or subapiculate to obtuse, base cuneate to angustate, sheathing or not, pairs united to form narrow interfoliar ridge; basal or near-basal veins (3)5–9, flabellate, branching and often visibly anastomosing distally, tertiary reticulation obscure or apparently absent; laminar glands dense, often





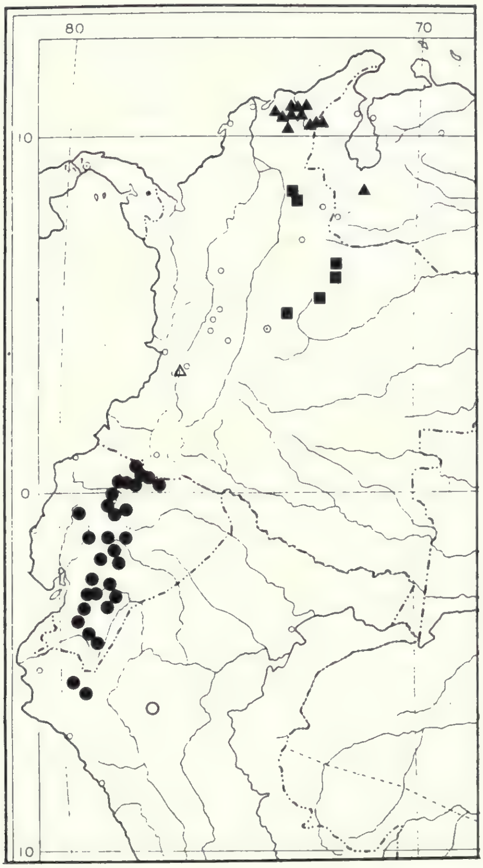
obscure beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from one or two nodes below; pedicel 4–12 mm long, incrassate upwards; upper leaves not transitional. *Flowers* 18–35 mm in diam., stellate to subcyathiform. *Sepals* (7)10–14 × (2)3–8 mm, elliptic-subcircular to elliptic-oblong or rarely oblong, acute to subacute; veins (5)7–11, dichotomising distally, with midrib not or slightly prominent; glands linear, distally punctiform. *Petals* bright yellow, 10–22 × 4–10 mm, *c.* 1·3–1·5 × sepals, obovate; apiculus acute; glands linear, distally punctiform. *Stamens c.* 40–90, longest 5–10 mm long, *c.* 0·5 × petals. *Ovary* (2·5)3–4 × 2–2·5 mm, ovoid-ellipsoid to subglobose; styles 3–4, (2)3–7 mm long, 1–1·75 × ovary, outcurving to diverging, stout; stigmas scarcely to broadly capitate. *Capsule* 5–8 × 4–6 mm, cylindric-ellipsoid, equalling sepals. *Seeds c.* 1·2 mm long, ecarinate; testa finely scalariform.

In open páramo; 3000–4300 m.



Colombia (César/Norte de Santandér to Boyacá). In the Cordillera Oriental from Cerro de Oroque to Vado Hondo. Map 13 (excluding Cundinamarca records, which belong to 55 *H. ruscoides*).

COLOMBIA. Arauca: Sierra Nevada del Cocuy, Quebrada El Playón, Agua Tendida, 3100 m, 10.vi.1973 (fl), *Cleef* 10174 (U). Boyacá: Sierra Nevada del Cocuy, near El Playón, *c.* 3800 m, 10.ix.1957 (fl), *Grubb, Curry & Fernandez-Perez* 777 (COL, K, US); Páramo de Chitá, cabeceras de Río Casanare, Km 93 de la carretera a La Punta, 3080 m, 19.vii.1972 (fl), *Cleef* 4744 (BM, U); Peña de Arnical, N. de Vado Hondo, 3600 m, 6.iv.1973 (fl), *Cleef* 9418 (U). César/Norte de Santandér: 20 km al S.



Map 13 31. *H. pimeleoides* ■; 32. *H. magdalenicum* ▲; 33. *H. valleanum* △; 34. *H. sprucei* •; 37. *H. wurdackii* ○.

de Abrego, Las Jurisdicciones (Cerro de Oroque), 3700–3900 m, 19–21.v.1969 (fl & fr), *Garcia-Barriga & Jaramillo* 19744 (COL). Norte de Santandér: Páramo de Las Jurisdicciones, SW. of Ocaña, 3000–3500 m, 8.vii.1984 (fl), *Wood* 4526 (K).

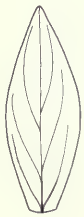
H. pimelioides shows a continuous morphological trend southwards from a tall form in the Cerro de Oroque with stout branches, large, sessile, sheathing leaves, and large flowers with long styles and scarcely broadened stigmas, to a relatively low form in the Vado Hondo area with slender branches, small, petiolate, not sheathing leaves, and small flowers with short styles and broad stigmas. In the Cerro de Oroque population the large sessile or subsessile leaves have up to 9 free basal veins and a thin margin, whereas in the Vado Hondo population the smaller petiolate leaves have only one vein (the midrib); but 1–2 pairs of midrib branches originate near the base, so that the venation is reduced-flabellate. This is in contrast to the leaf venation of plants in the Sierra Nevada del Cocuy and elsewhere in Boyacá that belong to *H. cardonae*. These have rather similar leaves, but they are relatively narrower and less crowded, the margin is not or only slightly indurated, and the midrib branches, where visible, arise at least one third of the distance from the base.

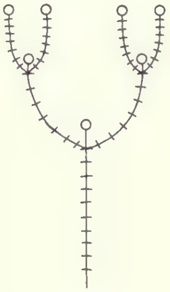
H. pimeleoides appears to be related to *H. magniflorum* and *H. stuebelii* because of its primitively broad-based leaves with flabellate venation and large flowers with 3–5 styles. It is the basic species to which the remainder of sect. *Brathys* is related, respectively through 32 *H. magdalenicum* and 49 *H. jaramilloi*.

32. **Hypericum magdalenicum** N. Robson, **sp. nov.**

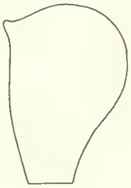
H. pimeleoidei Planchon & Linden ex Triana & Planchon affinis, sed foliis semper sessilibus angustioribus basi haud vel vix vaginatis venatione pinnata, sepalis plerumque angustioribus, ovario angustiori, stigmatibus haud vel vix capitatis, differt. Type: Colombia, Magdalena, Sierra Nevada de Santa Marta, quebrada from Laguna Río Frío, 3250 m, 28.vii.1972 (fl), *Kirkbride & Forero* 1748 (COL!, holotype; NY!, isotype).

Shrub (0·2–)0·7–1·5 m tall, erect, with branches strict, pseudo-dichotomous and sometimes with 2–3 laterals closely beneath flower. *Stems* orange-brown, 4-lined and compressed when young, the subfoliar ridges broad, soon terete, cortex exfoliating irregularly; internodes 2–4 mm long. *Leaves* sessile, densely imbricate, erect or outcurving, markedly tetrastichous, deciduous above base without fading; lamina 8–18 × 2–6·2 mm, broadly to rather narrowly elliptic or oblanceolate, plane to incurved-conduplicate, not or slightly cucullate, midrib plane or slightly impressed beneath, margin not distinct, epidermis sometimes undulate, concolorous, sometimes glaucous, ± thinly to thickly coriaceous; apex acute, base narrowly cuneate, scarcely sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, with *c.* 3–4 pairs of ascending lateral branches, sometimes branching distally, not prominent or impressed beneath, tertiary reticulation not visible; laminar glands ± dense, sometimes visible beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 4·5 mm long, not incrassate upwards; upper leaves not transitional. *Flowers* 20–30 mm in diam., stellate. *Sepals* (7–)9–11 × (2–)2·5–3 mm, elliptic, acute, veins *c.* 9–11, obscurely reticulating distally, with midrib not or slightly prominent; glands linear, punctiform near apex. *Petals* deep yellow, (10–)14–17 × (5–)9–11 mm, 1·5–2 × sepals, obovate; apiculus acute; glands linear, distally interrupted to punctiform. *Stamens c.* 100–120, longest *c.* 5–8 mm long, *c.* 0·5 × petals. *Ovary* 2·5–3 × 1·5–2 mm, ellipsoid to subglobose; styles 3, 6–7·5 mm long, 2·5–3·5 × ovary, spreading-incurving; stigmas narrow to narrowly capitate. *Capsule* (6–)8–9 × 4–6 mm, ellipsoid, shorter than sepals. *Seeds c.* 1·2 mm long, ecarinate; testa finely scalariform.





In páramo forest, scrub or damp grassland; 2400–4875 m.



Colombia (Magdalena), Venezuela (Zulia and Mérida). In the Sierra Nevada de Santa Marta and the Sierra de Perijá, with one probably conspecific record from the Páramo del Molino. Map 13.

COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, alredores de cabeceras de Río Sevilla, 3320–3410 m, 22.i.1959 (fl & fr), *Barclay & Juajibioy* 6620 (COL, MO, NY); Sierra Nevada de Santa Marta, valley of Río Yebosimeina, 3500–4000 m, 22.v.1977 (fl & fr), *Starker White & Alverson* 547 (COL, MO, NY); Sierra de Perijá, E. of Manaure, quebrada de Floridablanca, 2700–2800 m, 9–12.xi.1959, *Cuatrecasas & Romero Castañeda* 25171 (COL).

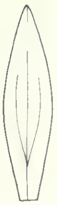
VENEZUELA. Mérida: Páramo del Molino, 2600 m, 19.i.1922 (fl), *Jahn* 940 (VEN). Zulia: Perijá, Cerro Fetari, iv.1952 (st), *Urbano* 2 (VEN).

H. magdalenicum differs from the sessile-leaved form of *H. pimeleoides* by (i) the leaves with pinnate venation but with a scarcely sheathing base and (ii) the narrower petals and sepals and usually shorter styles.

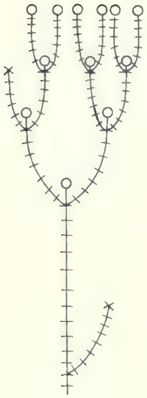
H. magdalenicum, which has a pivotal position in relation to over half the remaining species of sect. *Brathys* (Spp. 38–53), is rather variable. The nearest form to *H. pimeleoides* (from Sierra de Santa Marta, Río Sevilla) has relatively broad, plane leaves with conspicuous gland dots beneath. Most other forms from Sierra de Santa Marta, as well as those from Sierra de Perijá, have narrower, incurved-conduplicate leaves in which the gland dots are inconspicuous or superficially invisible (except in some Sierra de Perijá populations). Of these, the population from the Río Donachui area has stiffly erect, relatively thick stems and markedly imbricate leaves (tending towards 43 *H. parallelum* and 40 *H. bolivaricum*), whereas the other populations have more divergent, relatively thin stems and less markedly imbricate, though distinctly tetrastichous leaves (tending towards 50 *H. lancifolium* and its relatives).

33. **Hypericum valleanum** N. Robson, **sp. nov.**

H. sprucei N. Robson affinis, sed foliis latioribus, nec profunde incurvatis nec cucullatis, manifeste glanduloso-punctatis, pedicello 3–4 mm longo, stylis crassiusculis, differt. Type: Colombia, Valle de Cauca, Los Farallones, filo de la cordillera, matorrales de páramo en el cerro La Torre, *c.* 3750 m, 10.x.1944 (fl), *Cuatrecasas* 177861 (F!, holotype & isotype).



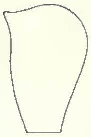
Shrub c. 1 m tall, erect, with branches strict, pseudo-dichotomous and lateral. *Stems* orange-brown, compressed? when young, soon subterete to terete, cortex exfoliating irregularly; internodes 1–2 mm long. *Leaves* sessile, subimbricate, narrowly spreading and twisting, subtetrastichous, deciduous above base without fading; lamina 11–17 × 2–3 mm, narrowly elliptic, shallowly incurved, not cucullate, midrib impressed, margin very narrowly hyaline, concolorous, not glaucous, coriaceous; apex sharply acute, base angustate, not sheathing, pairs united to form very narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense, large, visible beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel stout, 3–4 mm long; upper leaves not transitional. *Flowers c.* 20 mm in diam.?, stellate. *Sepals* 7–10 × 2–2·8 mm, narrowly elliptic to lanceolate, acute to acuminate, incurved above, margin narrowly hyaline, veins 5, the outer branched, midrib not or scarcely prominent; glands linear, distally punctiform. *Petals* bright (?) yellow, 10–12 × 5–6 mm, *c.* 1·2–1·4 × sepals, obovate; apiculus sharply acute; glands striiform to punctiform. *Stamens c.* 60 ?, longest 5–6 mm long, *c.* 0·5 × petals. *Ovary c.* 2 × 1·5 mm, ellipsoid; styles 3, *c.* 3 mm long, *c.* 1·5 × ovary, stout, suberect; stigmas narrow. *Capsule* and *seeds* not seen.



In páramo; 3750 m.

Colombia (Valle de Cauca). Known only from the type collection. Map 13 (p. 62).

COLOMBIA. Valle de Cauca: Cordillera Occidental, Los Farallones, cerro La Torre, *c.* 3750 m, 10.x.1944 (fl), *Cuatrecasas* 17861 (F).



H. valleanum is intermediate in form and distribution between the more primitive form of *H. magdalenicum* (with broad punctate leaves) and *H. sprucei*, differing from the former by its shorter styles and narrower leaves, and from the latter by its broader, thicker, and densely punctate not cucullate leaves and its stout styles and generally stronger habit. It appears to be a relict population.

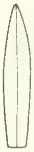
34. **Hypericum sprucei** N. Robson, **sp. nov.**

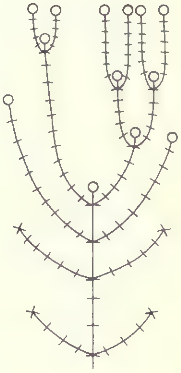
H. aciculari Kunth affinis, sed caulibus crassioribus, foliis latioribus et saepissime longioribus, coriaceis, sepalis petalisque longioribus, staminibus numerosioribus, differt. Type: Ecuador, Tungurahua, [Volcán] Tungurahua, 2400–3000 m, xi.1857 (fl), *Spruce* 5110 (BM!, holotype; c!, GH!, K!, P!, S!, isotypes).

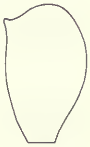
Hypericum struthiolifolium sensu R. Keller in *Bull. Herb. Boissier* II, **8**: 180 (1908) [‘*struthiolaefolium*’]; Gleason in *Bull. Torrey bot. Club* **56**: 102, 105 (1929), pro parte excl. typum.

Icon: Fig. 11.

Shrub 0·2–2 m tall, erect to ascending, with branches strict, lateral or more rarely pseudo-dichotomous. *Stems* orange-brown, 4-lined and ancipitous when young, eventually terete, cortex exfoliating irregularly; internodes 1·5–7 mm long. *Leaves* sessile, densely to loosely imbricate, erect, spreading and twisting, scarcely tetrastichous, deciduous above base without fading; lamina 6–12 × 0·8–1·7 mm, very narrowly oblanceolate to linear, incurved-cucullate, midrib impressed beneath, margin very narrowly hyaline, concolorous, not glaucous, coriaceous; apex acute, base parallel, not sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands rather dense, few or sometimes none visible beneath. *Inflorescence* 1-flowered, rarely with pseudo-dichotomous branches from node below; pedicel 1·5–3 mm long, not incrassate upwards; upper leaves not transitional. *Flowers* 20–30 mm in diam., stellate. *Sepals* 7–11 × 1·5–2·5 mm, lanceolate, acute to acuminate, incurved above, margin hyaline, veins 5, midrib not prominent; glands linear, distally punctiform. *Petals* bright to deep yellow, 10–15 × 5–7 mm, *c.* 1·4 × sepals, oblong-oblanceolate; apiculus sharply acute to apiculate; glands striiform to punctiform, sparse. *Stamens* 60–75, longest 5–9 mm long, 0·5–0·6 × petals. *Ovary* 2–3·5 × 1·5–2 mm, ellipsoid-subglobose; styles 3(4), (2·5)3–4·5 mm long, (1·3)1·5–2 × ovary, outcurving, slender; stigmas narrowly or not capitate. *Capsule c.* 5 × 3 mm, broadly ellipsoid to subglobose, shorter than sepals. *Seeds c.* 0·8 mm long (immature?), ecarinate; testa finely scalariform.







Open, dry or damp páramo; 2725–4000 m.

Ecuador (Carchi to Loja, apparently absent from Cotopaxi and Bolivar), Peru (Piura). Map 13 (p. 62).

ECUADOR. Azuay: *c.* 10 km NE. of Sevilla de Oro, 3000–3200 m, 13.ix.1976 (fl), *Øllgaard & Balslev* 9449 (AAU, BM, MO); ‘Oriente’ border, Eastern Cordillera between Oña and río Yacuambi, 3000–3360 m, 10–19.ix.1945 (fl & fr), *Prieto* P-297 (BM, NY). Cañar: between Biblian and Cañar, *c.* 3350 m, 21.ix.1955 (fl), *Asplund* 17665 (S). Carchi: Base of Volcán Chiles, km 34–36 on Tulcan – Maldonado road, 3900–4050 m, 19.v.1973 (fl), *Holm-Nielsen et al.* 5888 (AAU, F, GB, MO, S, U). Chimborazo: Atilio, *c.* 3700 m, 29.i.1968 (fl), *Harling, Storm & Ström* 6705 (GB). Imbabura: Ibarra to Mariano Acosta, at pass (Hacienda Yura Cruz), 3600–3800 m, 10.viii.1976 (fl & fr), *Øllgaard & Balslev* 8664 (AAU, BM, MO, U). Loja: Loja – Zamora road, 1 km east of pass (Km 12), 2725–2750 m, 17.iv.1973 (fl), *Holm-Nielsen et al.* K. 3698 (S). Morona-Santiago: Gualaceo–General Plaza (Limón) road, 3000–3100 m, 20.ic.1967 (fl), *Sparre* 18778 (S). Napo: Cordillera de Los Llanganati, Chihuila Sacho o Ainchilibi, *c.* 3750 m, 25–29.viii.1959, *Barclay & Juajibioy* 8996 (MO, NY); Sucumbios ‘Playon de San Francisco’, Camino al Cerro el Mirador, 3600–3800 m, 29.xii.1980 (fl), *Jaramillo & Coelle* 3903 (AAU, QCA). Pichincha: 15·4 km west of Papallacta, 3980 m, 26.iii.1972, *MacBryde & Dwyer* 1185 (MO). Tungurahua: Llanganati Mts, Lake Aucacocha, 3700 m, vii.1969, *Edwards* 58(K); Páramo of Minza Chica, 3800 m, 4.iv.1939 (fl), *Penland* 307 (F, GH). Zamora – Chinchipe: Loja to Zamora, 2800 m, 18.ix.1961, *Dodson & Thien* 685 (BM).

PERU. Piura: above Huancabamba, 3000 m, iv.1912 (fl), *Weberbauer* 6133 (F, GH, S).

H. sprucei provides a morphological and geographical link between *H. valleanum* (Colombia) and three species in southern Ecuador and Peru (Spp. 35–37). From *H.*

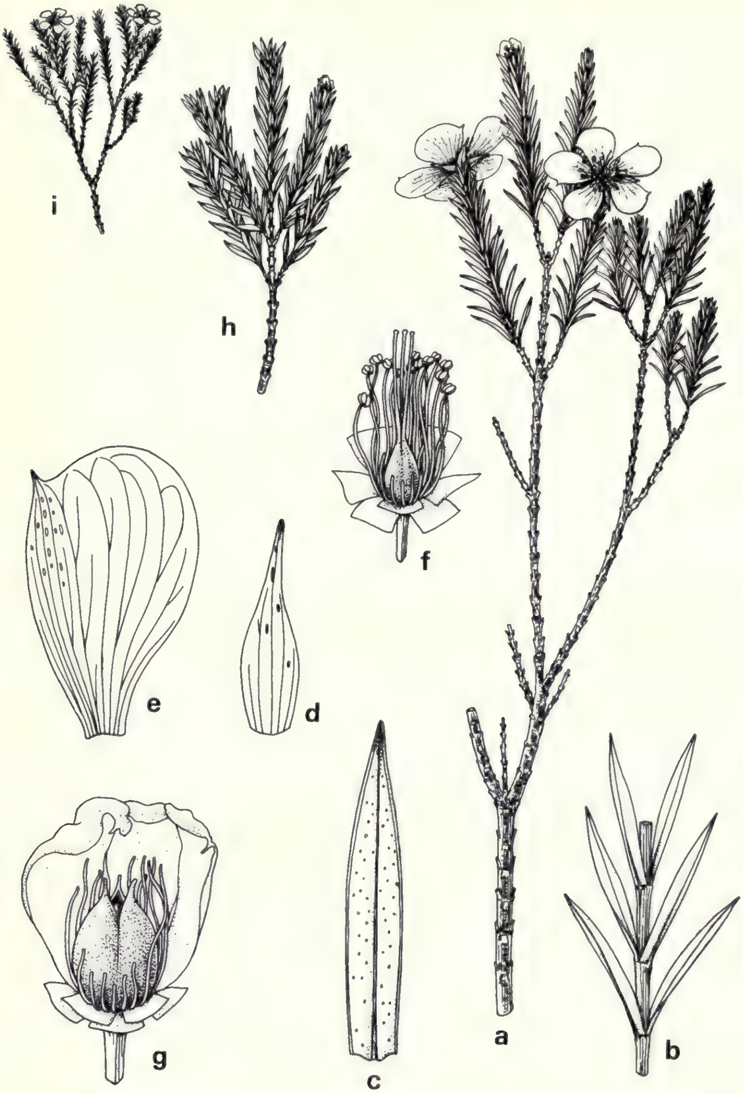


Fig. 11 A. *H. sprucei*: (a) habit; (b) stem with leaves; (c) leaf; (d) sepal; (e) petal; (f) stamens (partly cut away) and ovary; (g) capsule. B. *H. valleanum*: (h) habit. C. *H. aciculare*: (i) habit (a, h, i × ½; b × 2; c–g × 3). A. *Øllgaard & Balslev* 8454; B. *Cuatrecasas* 17861; C. *Hartweg* 719.

valleanum it differs in the slender styles and the shorter, narrower leaves. For differences between it and the southern species, see their accounts below.

H. sprucei varies clinally from north to south, the plants from Carchi being most similar to *H. valleanum*. Towards the southern end of its range (Azuay to Piura), the leaves become slenderer and more flexuous, and the habit low and multi-stemmed. In Chimborazo the leaves and flowers of some plants are relatively small, thus indicating a trend towards 35 *H. aciculare*.

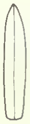
35. **Hypericum aciculare** Kunth

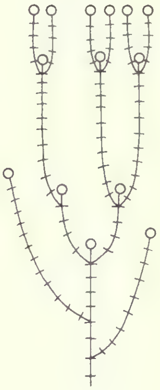
in Humboldt, Bonpland & Kunth, *Nova Gen. et Spec. Pl.* **5**: 190 (1822); Choisy in DC., *Prodr. syst. nat. regni veg.* **1**: 553 (1824); Jameson, *Pl. Aequator.* **1**: 108 (1865); R. Keller in *Bull. Herb. Boissier* II, **8**: 176 (1908) ? (see below), in Engler

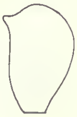
& Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925). Type: Ecuador, Loja, locis temporis prope Loxam (Regni Quitensi), 1908 m, viii.1805, *Humboldt & Bonpland* s.n. (P!, holotype; F!, US!, photographs)

H. struthiolifolium Juss. in *Annls Mus. Hist. nat. Paris* **3**: 160 (1804) [*'struthiolaefolium'*] pro parte, quoad var. innom. (p. 161, t. 16 f. 2 b).
H. struthiolifolium [var.] β sensu Choisy, *Prodr. monogr. fam. Hypéric.*: 59 (1821) [*'struthiolaefolium'*] pro parte, quoad spec. Peruv.
H. struthiolifolium [var.] β *minutum* Choisy in DC., *Prodr. syst. nat. regn. veg.* **1**: 533 (1824) [*'struthiolaefolium'*]. Type: Peru, *Dombey* s.n. (G, holotype; P!, isotype).
Brathys acicularis (Kunth) Spach, *Hist. nat. vég.* Phan. **5**: 366 (1836), in *Annls Sci. nat.* II, **5**: 366 (1836).
H. laricifolium sensu Bentham, *Pl. Hartweg.*: 126 (1843–1844).

Shrub 0·3–2 m tall, erect and bushy to decumbent and slender, with branches strict to ascending, lateral and frequently pseudo-dichotomous. *Stems* orange-brown, 4-lined and ± ancipitous when young, eventually terete, cortex exfoliating irregularly; internodes 1–7 mm long. *Leaves* sessile, subimbricate or not, suberect, outcurving and usually twisting, not or scarcely tetrastichous, deciduous above base without fading; lamina 3·5–7 × 0·4–0·6 mm, very narrowly elliptic to linear-acicular, incurved, slightly cucullate, midrib impressed beneath, margin very narrowly hyaline, concolorous, not glaucous, subcoriaceous to chartaceous; apex acute, base parallel-sided, not sheathing, scarcely broadening but pairs forming narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense to very sparse, visible beneath. *Inflorescence* 1-flowered, terminal, with pseudo-dichotomous branches from node below and terminating short unbranched lateral shoots; pedicel 1·5–2·5 mm long, not incrassate upwards; upper leaves not transitional. *Flowers* 10–17 mm in diam., stellate. *Sepals* 4–7·5 × 0·7–1·5 mm, narrowly lanceolate, acute, incurved above, margin hyaline, veins (3)5, midrib not prominent but whole sepal often becoming ribbed; glands linear, distally punctiform. *Petals* yellow or apricot to orange, sometimes tinged red, 6–10 × 3–7 mm, *c.* 1·5 × sepals, oblong-obovate, apiculus sharply acute; glands striiform to punctiform. *Stamens* 30–55, longest 3–5 mm long, *c.* 0·5 × petals. *Ovary* 1·5–2·5 × 1–1·5 mm, ellipsoid-subglobose; styles 3, 2·5–3(4) mm long, 1·2–2 × ovary, outcurving-ascending; stigmas narrow. *Capsule* 3·5–4 × 2·5–3·5 mm, broadly ellipsoid, shorter than sepals. *Seeds* 1·2 mm long, ecarinate; testa finely scalariform.







Dry, open scrub on slopes of páramo, dense moist forested slopes, and wet sphagnum; 1800–3700 m.

Ecuador (Azuay, Loja), Peru (Piura, Amazonas). Map 14 (p. 68).

ECUADOR. Azuay: Km 85 on Pan-American Highway north of Loja, 2850–2950 m, 3.v.1973 (fl), *Holm-Nielsen et al.* 4808 (AAU, F, GB, S, U); Río Collay south of El Pan, Huagrarancha slopes, 2650–3290 m, 6.vii.1943 (fl), *Steyermark* 53372 (F); *30–50 km S. of Cuenca, Páramo de Tinajillas; 3300–3450, 17.iii.1945, *Camp* E-2229 (BM, NY);* Rancho Ovejero, *c.* 3000 m, 1–2.viii.1969 (fl). *Barclay & Juajibioy* 8484 (NY). Loja: between La Toma and Loja, 1800–2600 m, 4.ix.1923 (fl), *Hitchcock* 21431 (GH, NY, US);* 7 km from Loja on road to Zamora, 2350 m, 8.ix.1959 (fl), *B. & C. Maguire* 61667 (BM, NY);* W. slopes of Cerro Villonaco, 2200–2250 m, 10.iv.1974 (fl & fr), *Harling & Anderson* 13351 (GB, NY).

PERU. Piura: Huancabamba to Cuello del Indio, Mitopampa, 2650 m, 22.vii.1975 (fl), *Sagástegui, Cabanillas & Díos* 8253 (MO). Amazonas:* Chachapoyas, 3–6 Km W. of Molinopampa, 2200–2450 m, 19.vii.1962 (fl), *Wurdack* 1403 (F, K, NY, S, US). *Pajonales, Pozuro, 3000 m, vii.1863 (fl), *Pearce* 252 (BM, K).

H. aciculare differs essentially from *H. sprucei* in habit and size of parts. It most resembles some populations of the latter from Chimborazo, from which it is separated by a disjunction of merely *c.* 100 km. Other, less similar populations of *H. sprucei*, however, are found in the same area as *H. aciculare*, which occurs in two ecologically somewhat distinct forms with widely overlapping areas of distribution. If

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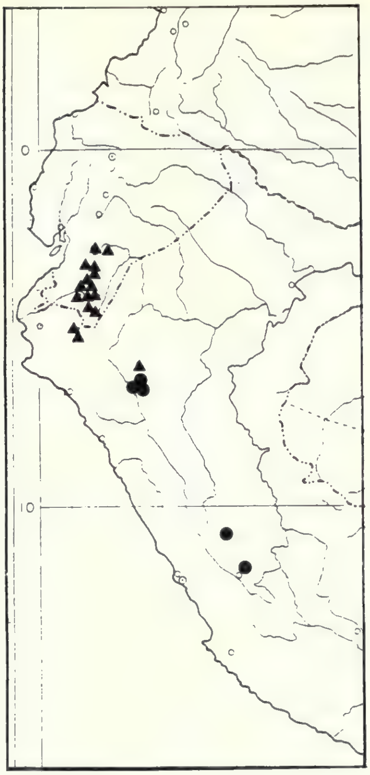
* Wet habitat form, see p. 68.



Map 14 35. *H. aciculare* ▲; 36. *H. recurvum* ●.

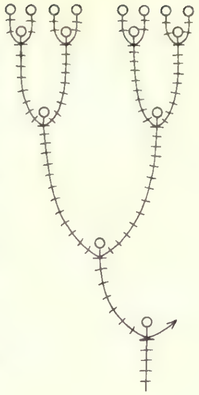
these forms prove to be genetically distinct, it may be possible to recognize them as subspecies, as they are almost always distinguishable from one another. Plants on open or forested páramo slopes are bushy with branching mostly pseudo-dichotomous, whereas those in marshes and seepages are slender with branching mostly lateral (records marked*).

Keller (1908 supra) keys out *H. aciculare* with *H. nitidum* Lam. as having connate styles. If his material did indeed belong to this species, then he must have interpreted it wrongly.

36. **Hypericum recurvum** N. Robson, **sp. nov.**

H. sprucei N. Robson affinis, sed foliis aureo-marginatis apice longe acuminatis, recurvascentibus haud torquescentibus, petalis angustioribus, differt; a *H. aciculari* Kunth isdem characteribus differt. Type: Peru, Amazonas, Chachapoyas, middle eastern Calla-Calla slopes, near Kms 416–419 of Leimebamba-Balsas road, 2900 –3100 m, 9.vii.1962 (fl & fr), *Wurdack* 1303 (K!, holotype; F!, GH!, NY!, P!, S!, US, isotypes).

Shrub 0·15–0·7 m tall, many-stemmed, erect or decumbent and rooting, with branches strict, pseudo-dichotomous and sometimes lateral. *Stems* orange- to reddish-brown, 6-lined when young, eventually terete, cortex exfoliating in irregular flakes; internodes 1–3 mm long. *Leaves* sessile, imbricate-suberect but not markedly tetrastichous at first, eventually becoming markedly outcurved but not twisted, deciduous above the base after turning brown; lamina 5–8 × 0·8–1·2 mm, subulate, distally conduplicate and ± cucullate, otherwise incurved with midrib slightly prominent proximally to slightly impressed beneath, margin narrowly glaucous, chartaceous; apex acicular, base broadened, markedly sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands rather dense,

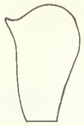


visible beneath when young. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 3·5–5 mm long, not incrassate upwards; upper leaves not transitional. *Flowers* 15–20 mm in diam., stellate. *Sepals* 7–9 × 1–1·5 mm, narrowly-lanceolate-acerose, long-acuminate, cucullate, with golden-hyaline margin; veins 3–5, unbranched, not prominent; glands linear, interrupted in distal 1/4. *Petals* golden yellow, 8–12 × 2·5–4 mm, 1·2–1·4 × sepals, narrowly obovate-oblong; apiculus acicular; glands linear, distally interrupted. *Stamens c.* 60, longest 6–8 mm long, *c.* 0·7 × petals. *Ovary* 2·5–3 × 1–1·2 mm, narrowly ellipsoid; styles 3, 4–5 mm long, *c.* 1·7 × ovary, outcurved-ascending; stigmas narrow to scarcely capitate. *Capsule* 3–5 × 2–3 mm, ellipsoid, shorter than sepals. *Seeds* 0·7–0·8 mm long, ecarinate; testa finely scalariform.

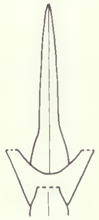
On open hillsides in exposed and (in Pasco) boggy areas; 2700–3100 (?–3300) m.

Peru (Amazonas (Chachapoyas), Junin, Pasco), apparently almost restricted to the Cerro Calla-Calla. Map 14.

PERU. Amazonas: Chachapoyas, Cordillera Calla-Calla between Leimebamba and Balsas, 2900–3000 m, 21.viii.1963 (fl), *Ferreyra & Acleto* 15284 (NY); between Leimebamba and Balsas, 2700 m, 1.vi.1963 (fl & fr), *López, Sagástegui & Callantes* 4429 (NY); Cerro Calla-Calla, E. side, 19 km above Leimebamba on Balsas road, 3100 m, 4.vi.1964 (fl), *Hutchinson & Wright* 5505 (F, NY, UC, US); Jalca de Calla-Calla, 3100 m, 7.v.1970 (fl & fr), *Sagástegui* 7451 (F, NY, VEN); Chachapoyas to Moyobamba, La Jalca, 2700–3300 m, 20.i.1930 (fl), *Williams* 7583 (F, NY); Chachapoyas, 1826 (fl & fr), *Mathews* 2130 (BM, K, P). Junin: Huancayo, Quebrada Occopilla, ii.1948 (fl), *Soukoup* 3636 (MO). Pasco: Oxapampa, Cordillera Yanachaga, Cerro Pajonal 12 km SE. of Oxapampa, 2700–2800 m, 7.x.1982 (fr), *Foster* 8992 (BM, MO).

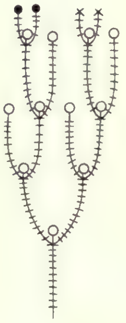


H. recurvum is clearly related to the southern, low, many-stemmed form of *H. sprucei*, differing from it mainly in the often glandular, acuminate leaves, which becomes recurved, not twisted, and are suffused with a golden tint (at least when dried). The longer styles and narrower, acuminate sepals distinguish *H. recurvum* from *H. andinum*, which has an overlapping area of distribution.

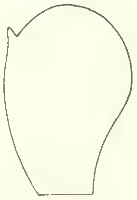


37. **Hypericum wurdackii** N. Robson, **sp. nov.**

H. recurvo N. Robson affinis, sed foliis longioribus, carinatis, densissime imbricatis, valde tetrastichis alas formantibus, floribus maioribus, differt; a *H. aciculare* Kunth isdem characteribus differt. Type: Peru, Amazonas, Chachapoyas, summit of Cerro Malcabal (Cerro Tumbe), 3–6 km SW. of Molinopampa, 2850–2900 m, 20.vii.1962 (fl & fr), *Wurdack* 1426 (K!, holotype; F!, GH!, MICH!, NY!, P!, S!, US, isotypes).



Shrub 0·15–0·3 m tall, several-stemmed, erect, with branches strict, pseudo-dichotomous and sometimes lateral. *Stems* orange-brown, completely enclosed by leaves when young, eventually terete, cortex exfoliating irregularly; internodes 1 mm long. *Leaves* sessile, imbricate, markedly tetrastichous with the vertical rows winglike, not or scarcely outcurving, not twisted, deciduous above the base after turning brown; lamina 9–14 × 1–2 mm, linear-acerose, incurved-conduplicate, cucullate, carinate wholly or only at apex and base, margin narrowly golden-hyaline especially towards base, otherwise concolorous, yellow-green, not glaucous, chartaceous; apex sharply acute, base broadened, markedly sheathing, pairs united to form deep interfoliar ridge; basal vein 1, unbranched; laminar glands dense, invisible below in mature leaf. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 2–3 mm long, not incrassate upwards; upper leaves not transitional. *Flowers* 20–25 mm in diam., stellate. *Sepals* 10–12 × 3–4 mm, lanceolate-acerose, sharply acute, not cucullate, with golden-hyaline margin; veins 7, unbranched, not or scarcely prominent; glands linear, punctiform in upper half. *Petals* golden (?) yellow, 15–18 × 7–8 mm, *c.* 1·5 × sepals, narrowly obovate; apiculus acute; glands linear, distally interrupted. *Stamens c.* 100, longest 8–9 mm long, *c.* 0·5 × petals. *Ovary c.* 2·5 × 1·5 mm, ellipsoid; styles 3, 4–5 mm long, 1·7–2 × ovary, outcurved-ascending; stigmas narrow. *Capsule c.* 6 × 3·5 mm, ellipsoid, shorter than sepals. *Seeds* not seen.



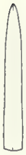
No habitat data known; 2850–2900 m.

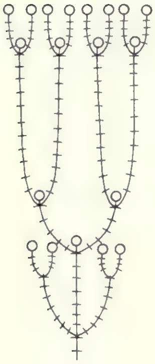
Peru (Amazonas-Chachapoyas). Known only from type collection. Map 13 (p. 62).
PERU. Amazonas: Chachapoyas, summit of Cerro Malcabal (Cerro Tumbe), 3–6 km SW. of Molinopampa, 2850–2900 m, 20.vii.1962 (fl & fr), *Wurdack* 1426 (F, GH, K, MICH, NY, P, S, US).

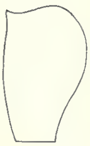
This bizarre species, which resembles a large *Cassiope tetragona* in habit, is clearly related to the low, many-stemmed form of *H. sprucei* from Piura. Although it is larger in all parts than *H. recurvum*, it can be interpreted as carrying the trends in leaf form and arrangement of that species a stage further. The leaves are even more closely imbricate, so that the tetrastichy characteristic of the young shoots of *H. recurvum* is very marked in *H. wurdackii*.

38. **Hypericum costaricense** N. Robson, **sp. nov.**

H. sprucei N. Robson affinis, sed foliis subcoriaceis saepe glaucis, apice haud vel vix cucullatis, floribus minoribus, sepalis apice acutissimis, stylis brevioribus, stigmatibus anguste vel late capitatis, capsula ovoidei-ellipsoideis, differt. Type: Costa Rica, Alajuela, upper slopes of Volcán Poás, *c.* 2700 m, 1.ix.1968 (fl & fr), *Wilbur & Stone* 10634 (BM!, holotype; DUKE!, NY!, US!, isotypes).



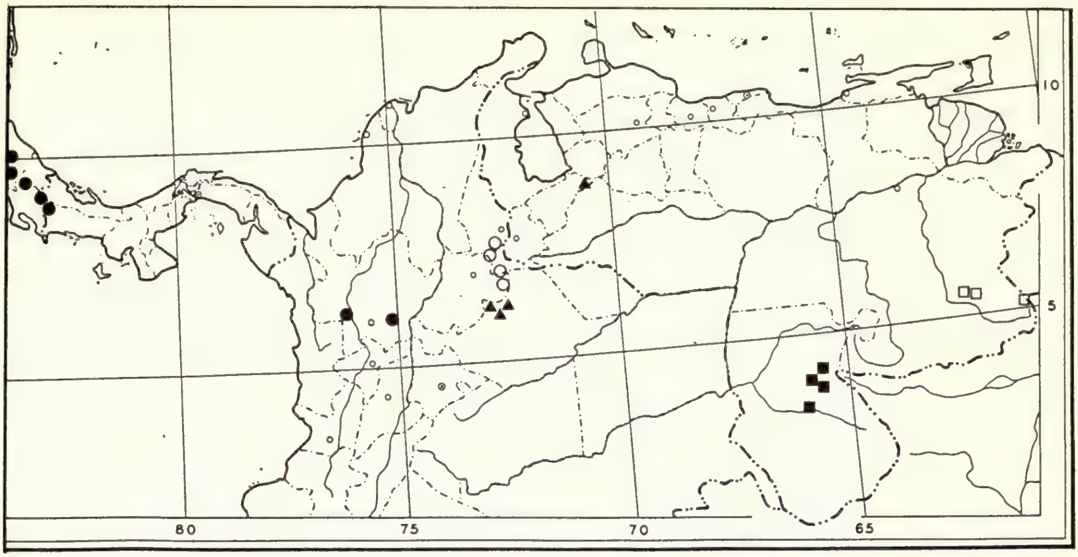




Shrub or shrublet c. 0·1–1 m tall, erect or ascending, forming dense rounded clumps, with branches strict, pseudo-dichotomous and lateral. *Stems* orange-brown, 4-angled and (?) ancipitous when young, eventually terete, cortex exfoliating in strips; internodes 2–4 mm long. *Leaves* sessile, ± imbricate to suberect, spreading to outcurving and twisting, ± markedly tetrastichous when young, deciduous above base without fading; lamina 5–15 × 0·6–1 mm, linear-elliptic to linear, incurved-canaliculate, not or scarcely cucullate, midrib impressed beneath, margin narrowly hyaline, concolorous, lucent or often glaucous, subcoriaceous; apex acute to subacute, base parallel-sided, scarcely broadening, pairs forming narrow interfoliar ridge; basal vein 1, unbranched; laminar glands ± dense, visible beneath. *Inflorescence* 1-flowered, terminal, with pseudo-dichotomous branches from node below; pedicel 3–4 mm long, rather slender, not incrassate upwards; upper leaves not transitional. *Flowers* 15–20 mm in diam., stellate. *Sepals* 5–8 × 0·8–1·6 mm, narrowly oblong to narrowly triangular-lanceolate, sharply acute, margin hyaline, veins 5(7), unbranched, midrib or all sometimes prominent; glands linear, distally punctiform. *Petals* bright yellow to orange-yellow, (6·5–)8–13 × 3–4 mm, *c.* 1·3–1·5 × sepals, oblong-obovate; apiculus sharply acute; glands linear, distally punctiform. *Stamens c.* 40–50, longest 5–6 mm long, *c.* 0·65 –0·75 × petals. *Ovary c.* 1·5–2 × 1–1·5 mm, ellipsoid; styles 3, 1·5–2 mm long, 0·7–1·5 × ovary, erect; stigmas narrowly to broadly capitate. *Capsule* 4–5 × 2·5–3 mm, ovoid-ellipsoid, obtuse to rounded, shorter than sepals. *Seeds* 0·7–1 mm long, ecarinate; testa finely scalariform-reticulate.

In open páramo on rocky, often volcanic slopes; (900–)2440–3700 m.

Costa Rica (San José, Alajuela, Cartago, Limón, Puntas Arenas), Panama (Chiriquí, Bocas del Toro), Colombia (Bolivar, Antioquía). Map 15.
COSTA RICA. Alajuela: upper slopes of Volcán Poás, *c.* 2700 m, 1.ix.1968 (fl & fr), *Wilbur & Stone* 10634 (BM, DUKE, GH, MO, NY, US). Cartago: Asunción of Cerro de la Muerte, *c.* 3150 m, 17.v.1971 (fl), *Wilbur* 14563 (DUKE, MICH, MO). Limón: Chirripó National Park, between Casa da Administración and peak, *c.* 3400 m, 13.ii.1983 (fl & fr), *Garwood et al.* 1162 (BM). Puntarenas/Bocas del Toro (Panama): Cordillera de Talamanca, Cerro Echandi, on the International border, 3050–3160 m, 22.viii.1983 (fl), *Davidse et al.* 2389 (BM, MO).
PANAMA. Bocas del Toro: Valle de Silencia, 2440 m, 8.viii.1979 (fl & fr), *Antonio* 1547 (BM, MO). Chiriquí: Cerro Fabrega and vicinity, near Costa Rican frontier, 3150–3335 m, 7–8.iv.1976 (fl), *Weston* 10149 (MO).
COLOMBIA. Antioquía: Páramo Frontino, near Llano Grande, 3450 m, 25.x.1976 (fl & fr), *Boeke & McElroy* 229 (NY), Bolivar/Antioquía: Páramo de Chaquiro, 900–960 m, 23.ii.1919 (fl & fr), *Pennell* 4285 (GH, NY).



Map 15 38. *H. costaricense* ●; 39. *H. bryoides* ○; 44. *H. marahuacanum*: a. subsp. *marahuacanum* ■, b. subsp. *strictissimum* ▲, c. subsp. *chimantaicum* □.

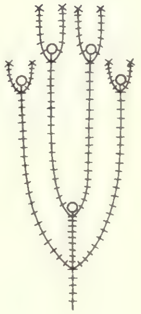
H. costaricense is related to 34 *H. sprucei*, having similar markedly incurved leaves that twist when long enough to do so, but they are not cucullate and no more than subcoriaceous. Moreover, the flowers are smaller, with shorter styles and capitate stigmas.

In a specimen from the highest point of the Pan-American Highway on the Talamanca Range (*J. & C. Taylor* 11757 (NY)) the leaves are broader, the flowers larger, and the styles longer than in the other specimens. It seems probable that the suggestion on the label is correct, i.e. that it is the hybrid *H. irazuense* × *H. costaricense*. The two Colombian collections belong to *H. costaricense* despite the disjunct distribution and the lower altitude of *Pennell* 4205, which is a dwarf shrub (0·1–0·15 m tall) with numerous lateral branches, leaves relatively long (*c.* 10 mm), recurving markedly and twisting, flowers that are relatively small for the species but nevertheless fall within its range of variation, and stigmas that are broadly capitate. It resembles a dwarf version of the (primitive) Panamanian form of *H. costaricense* and appears to be a reduction along a different line from that leading to *H. bryoides*. The other Antioquía collection (*Boeke & McElroy*) is taller but otherwise similar.

39. **Hypericum bryoides** Gleason

in *Bull. Torrey bot. Club* **56**: 102 (clav.), 103 (1929). Type: Colombia, Santandér, Páramo de Santurbán, 3000 m, 18.ii.1927 (fl), *Killip & Smith* 19533 (NY!, holotype; GH!, US!, isotypes).

Suffrutex 0·09–0·15 m tall, erect or ascending from creeping branching and rooting base, forming dense *Polytrichum*-like rounded clumps, with branches strict, pseudo-dichotomous and lateral. *Stems* orange-brown, 4-angled and(?) ancipitous when young, soon terete, cortex exfoliating irregularly; internodes 1–3·5 mm long. *Leaves* sessile, imbricate, eventually outcurving and slightly twisting, tetrastichous, deciduous above base without fading; lamina 3–5 × 0·–0·8 mm, linear-subulate, incurved-canaliculate, cucullate, midrib impressed beneath or not, margin narrowly hyaline, concolorous, not glaucous, chartaceous; apex subacute to obtuse, base gradually broadened and sheathing, pairs forming relatively broad interfoliar ridge; basal vein 1, unbranched; laminar glands dense, visible beneath. *Inflorescence* 1-flowered, terminal, with pseudo-dichotomous branches from node below; pedicel *c.* 1 mm long, relatively stout; upper leaves not transitional. *Flowers* 6–8 mm in diam., obconic (?). *Sepals* 3–5 × 0·7–1·3 mm, narrowly oblong to narrowly



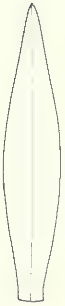
oblong-lanceolate, acute, incurved above, margin hyaline, veins 3–5, unbranched, midrib or all prominent; glands all linear or distally punctiform. *Petals* bright yellow, 3·5–6·5 × 1·5–3 mm, *c.* 1·2–1·4 × sepals, obovate; apiculus acute or obsolete; glands striiform. *Stamens* 20–35, longest 2·5–3 mm long, *c.* 0·75 × petals. *Ovary* 0·8–1 × 0·6–0·8 mm, ellipsoid; styles 3, 1–1·2 mm long, *c.* 1·2 × ovary, erect; stigmas narrowly to broadly capitate. *Capsule* 4–4·5 × 2–2·5 mm, cylindric-ellipsoid, subacute to obtuse, slightly exceeding sepals. *Seeds* not seen.

Rocky places in open páramo; 3000–4200 m.

Colombia (Norte de Santandér, Santandér, Boyacá). Map 15 (p. 71).
COLOMBIA. Boyacá: Sierra Nevada del Cocuy, Alto La Cueva, 3850 m, 5.vi.1973, *Cleef* 10000 (BM, COL, U). Norte de Santandér: Páramo de Romeral, 3800–4200 m, 30.i.1927 (st), *Killip & Smith* 18631 (F, GH, K, NY, S, US); Páramo de Santurbán, 5 km E. of Berlin, 3200 m, 4.vii.1984 (fl), *Wood* 4504 (K). Santandér: Páramo de Almorzadero, 3500–3700 m, 20.vii.1940 (fl), *Cuatrecasas & Garcia Barriga* 9993 (F), 9995 (COL), 9996 (NY).

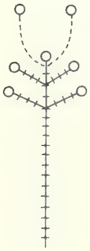
H. bryoides is a reduced suffruticose version of the more specialized form of *H. costaricense*, differing from it essentially in size of parts. The dense moss-like clumps expand by the creeping and rooting of the outer shoots.

40. **Hypericum bolivaricum** N. Robson, **sp. nov.**



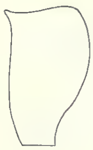
H. magdalenico N. Robson affinis, sed foliis angustissime ellipticis basi angustatis saepe terminantibus, petalis brevioribus, staminibus paucioribus, stylis brevioribus stigmatibus manifeste capitatis, differt. Type: Colombia, Bolívar, headwaters of Río Sinu, 1918 (fl), *Pennell* 4783 (NY!, holotype).

Shrub, with branches strict, lateral. *Stems* orange-brown?, 4-angled when young, the subfoliar ridges broad, eventually terete, cortex exfoliating in scales; internodes 1·5–2·5 mm long. *Leaves* sessile, subimbricate at first, spreading and twisting, scarcely tetrastichous, deciduous above base without fading; lamina 15–20 × 3–3·5 mm, very narrowly elliptic, incurved, not cucullate, midrib not prominent beneath, margin very narrowly hyaline, not glaucous, coriaceous; apex acute, pungent, base angustate, scarcely sheathing, united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands rather sparse, not or scarcely visible beneath; marginal glands dense, small. *Inflorescence* 1-flowered, probably with pseudo-dichotomous branches from node below; pedicel *c.* 2 mm long; upper leaves not transitional. *Flowers c.* 15 mm ? in diam., stellate? *Sepals* 9–11 × 2–3 mm, oblanceolate-oblong to narrowly oblong, acute, margin narrowly hyaline; veins 5–7, unbranched, not prominent; glands linear, punctiform in upper two-fifths. *Petals* yellow, *c.* 12 × 6 mm, *c.* 1·1 × sepals, obovate-oblong; apiculus acute; glands mostly striiform to punctiform. *Stamens* 34, longest 5–6 mm long, *c.* 0·5 × petals. *Ovary* 3 × 2 mm, narrowly ellipsoid; styles 3, 4·5 mm long, 1·5 × ovary, slightly outcurved; stigmas rather broadly capitate. *Capsules* and *seeds* not seen.



No habitat or altitude cited.

Colombia (Bolivar). Known from only one collection. Map 16 (p. 74).
COLOMBIA. Bolivar: headwaters of Río Sinu, 1918 (fl), *Pennell* 4783 (NY).



Although only one specimen of *H. bolivaricum* has so far been studied, its taxonomic position is clear and it is quite distinct from its nearest relatives. Morphologically and geographically it is intermediate between the long-leaved form of *H. magdalenicum* and the *H. juniperinum* group, having the thickly coriaceous leaves of the former but the 1-nerved, twisting leaves and predominantly lateral flowers of the latter.

41. **Hypericum juniperinum** Kunth

in Humboldt, Bonpland & Kunth, *Nova Gen. et Sp. Pl.* **5**: 189 (1822); Bentham, *Pl. Hartweg.*: 165 (1845). Type: Colombia, Cundinamarca ?, 'in frigidis Andium Nova-Granatensium', vii.1805 (fl & fr), *Humboldt & Bonpland* (P-HUM!, holotype; P! (F!, photograph), GH!, isotypes).

Brathys juniperina L. f., *Suppl. Pl.*: 268 (1781). Type: Colombia, Cundinamarca, 'in Nova Granada', *Mutis* (LINN!, holotype; BM!, MA!, US!, isotypes).

H. brathys Sm., *Plant. Ic. Ined. Herb. Linn.* **2**: 41, t. 41. (1790), nom. illegit.; Lam., *Encycl. méth.* (Bot.) **4**: 152 (1797); Choisy, *Prodr. monogr. fam. Hypéric.*: 59 (1821); Kunth in Humboldt, Bonpland, Kunth, *Nova Gen. et Spl. Pl.* **5**: 188 (1822); Choisy in DC., *Prodr. syst. nat. regni veg.*: **1**: 554 (1824); Bentham, *Pl. Hartweg.*: 165 (1845); Weddell, *Chloris Andina* **2**: 270 (1857); Treviranus, *Hyper. Animad.*: 15 (1861); Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 292 (1862); R. Keller in *Bull. Herb. Boissier* II, **8**: 177 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Knuth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 484 (1927); Gleason in *Bull. Torrey bot. Club* **56**: 102 (1929); Cuatrec. in *Trab. Mus. nac. Cienc. nat. Jard. bot. Madrid* (Bot.) **33**: 85 (1936). Type: as for *Brathys juniperina* Linn. f.

H. brathys [var.] β *juniperinum* (Kunth) Choisy in DC., *Prodr. syst. nat. veg.* **1**: 554 (1824); Weddell, *Chloris Andina* **2**: 270 (1857); Knuth in *Reprium Spec. nov. Regni veg.*, Beih. **43**: 483 (1927).

Brathys juniperina (Kunth) Spach, *Hist. nat. vég.* Phan. **5**: 450 (1836), in *Annls Sci. nat.* (Bot.) II, **5**: 366 (1836), non Linn. f. (1781).

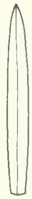
H. pseudobrathys Turcz. in *Bull. Soc. Nat. Moscou* **31** (1): 387 (1858) ['*pseudo-brathys*'] pro parte, quoad lectotypum et *Linden* 1242. Type: Venezuela, Mérida, 'in Sierra Nevada', 3000 m, 1846 (fl), *Funck & Schlim* 1140 (LE, lectotype; BM!, P! (GH!, photograph), W!, syntypes).

H. jahnii R. Keller in *Bot. Jahrb.* **58**: 196 (1923), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Gleason in *Bull. Torrey bot. Club* **56**: 103 (1929); Steyermark in *Fieldiana Bot.* **28**: 988 (1957). Type: Venezuela, Táchira, Páramo de Batallón, 3000 m, iii.1911 (fl), *Jahn* 2 (B†, holotype; NY!, US!, isotypes, F!, GH!, NY!, photographs).

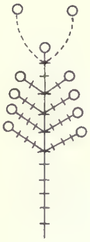
H. struthiolifolium var. *congestiflorum* sensu Knuth in *Reprium Spec. nov Regni veg.* Beih. **43**: 484 (1927) ['*struthiolaefolium*'] pro parte, quoad *Funck & Schlim* 1140.

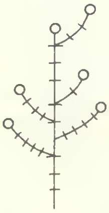
H. holtonii Gleason in *Bull. Torrey bot. Club* **56**: 104 (1929) ['*holtoni*']. Type: Colombia, Cundinamarca, 'in montibus juxta Bogotam', 10.xi.1852 (fl & fr), *Holton* 787 (NY!, holotype; GH!, K!, isotypes).

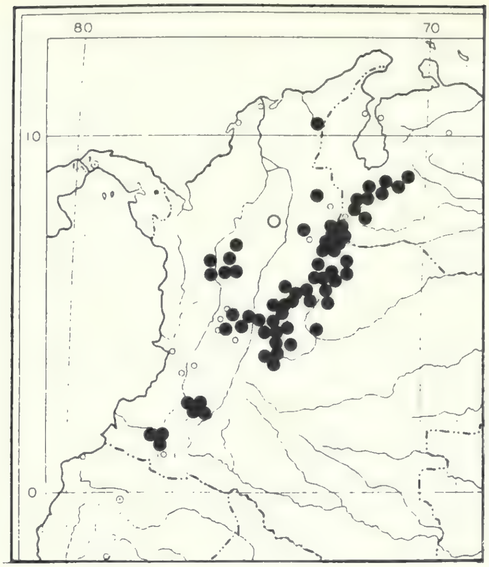
H. strictum var. *reductum* Gleason in *Bull. Torrey bot. Club* **56**: 104 (1929). Type: Colombia, Santandér, west slope of the Páramo de Santurbán towards Tona, 3000 m, 18.ii.1927 (fl & fr), *Killip & Smith* 19534 (NY!, holotype).



Shrub or shrublet 0·2–2·5 m tall, erect or rarely decumbent and rooting at the base, with branches strict, lateral or sometimes pseudo-dichotomous. *Stems* orange-brown, 4-angled and ancipitous when young, soon 2-lined, eventually terete, cortex exfoliating irregularly; internodes 1·5–10 mm long. *Leaves* sessile, not or scarcely imbricate, erect to spreading and twisting, not or scarcely tetrastichous, deciduous above base without fading; lamina 6–14 × 0·–1·5 mm, linear to acicular, rarely cucullate, midrib impressed beneath, margin narrowly hyaline, concolorous, rarely glaucous, coriaceous to subcoriaceous; apex acute, base parallel-sided, scarcely broadening, pairs forming narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense to sparse, sometimes visible beneath. *Inflorescence* 1-flowered, terminal (usually) and on up to 12 short lateral shoots, sometimes with pseudo-dichotomous branches from terminal node; pedicel 0·5–3 mm long, not incrassate upwards; upper leaves transitional. *Flowers* 4–12 mm in diam., stellate to obconic. *Sepals* 2·5–7 × 0·5–2 mm, narrowly lanceolate, acute, veins 5, unbranched, midrib not prominent, margin hyaline; glands linear, sometimes distally punctiform. *Petals* bright to pale yellow, (3–)4–9 × 1·5–3(–3·5) mm, 1·3–2·1 × sepals, narrowly oblong-obovate to obovate; apiculus acute to apiculate; glands mostly linear to mostly punctiform. *Stamens* 20–75, 3–5 mm long, longest 0·5–0·75 × petals. *Ovary* 0·8–3 × 0·6–1·8 mm, broadly ellipsoid or broadly ovoid to globose; styles 3–5(6), 1–3 mm long, 0·5–1·5 × ovary, ascending; stigmas narrowly to broadly capitate. *Capsule* 2·5–4 × 2–3 mm, ovoid-subglobose to globose, shorter than sepals. *Seeds* 0·6–1·2 mm long, ecarinate; testa finely scalariform.







Map 16 40. *H. bolivaricum* ○; 41. *H. juniperinum* ●.

In open forest, forest margins and damp or shaded areas in páramo and subpáramo; (1800) 2200–3800 m.

Venezuela (Trujillo, Mérida, Táchira), Colombia (Magdalena and Norte de Santandér to Putumayo). Map 16.

COLOMBIA. Antioquía: Páramo de Urrao, 3500 m, ix.1960 (fl), *Espinal & Perez* 258 (COL); 1 km norte de Santa Rosa de Osos, *c.* 2600 m, 25.ix.1948 (fl & fr), *Perez & Barkley* 18A058 (COL, NY); Páramo Frontino, near Llano Grande, 3450 m, 25.v.1976 (fl & fr), *Boeke & McElroy* 219 (MO, NY). Boyacá:* between Soatá and Cocuy, Páramo del Alto del Cañutal, 3300–3400 m, 8.ix.1938 (fl & fr), *Cuatrecasas* 1197 (F); Sierra Nevada del Cocuy, between Praton and Cobugon, *c.* 3100 m, 15.viii.1957 (fl), *Grubb, Curry & Fernandez-Perez* 507 (COL, K); Guicán, Hoya del río Tabor, en direccione a Ritacuva, 3570–3530 m, 18.ix.1969 (fl), *Cuatrecasas & Rodriguez* 27833 (BM, COL, US); Páramo de la Rusia, NW.-N. de Duitama, cerca del puente de río Surbá, 3240 m, 9.xii.1972 (fl & fr), *Cleef* 6925 (COL, U); carreteria Sogamoso-Pajarito, Km. 57–73, 2850–3010 m, 20.ix.1969 (fl), *Díaz* 196 (COL). Caldas: cabeceras del río Otún, hacia el Nevado de Santa Isabel, Bagas de la Laguna Negra (Quebrada de la Leona), 3800–3750 m, 24.xi.1946 (fl), *Cuatrecasas* 23159 (BM, F, P, U). Cuaca: Valley of Río Cofre, near Gabriel López, *c.* 3100 m, 14.x.1961 (fl & fr), *Cuatrecasas & Willand* 26431 (COL); Páramo de Guanaco, 1843 (fl), *Hartweg* 926 (BM, K, P, W);* Macizo Colombiano, Valle de Las Papas, alredores de Valencia, Los Andes, margens del rí Sucubun, 2910 m, 11.ix.–1.x.1958, *Idrobo, Pinto & Bischler* 3725 (COL, P). Cundinamarca: Macizo de Bogotá, El Retiro, Bogotá, 2600–2700 m, (v.1946 (fl & fr), *Schultes* 7004 a (COL, F, GH); Bogotá to Choachí, 27 km W. of Choachí, 3260 m, 4.i.1976 (fl), *Luteyn* 4730 (BM, COL, MO, NY); Páramo de Guasca, 2840 m, 15.xii.1938 (fl), *Balls* 5680 (BM, COL, F, K); Páramo de Sibaté, 3570 m, 22.xi.1981 (fr), *Inglesias* 19 (COL); entre Bogotá y La Calera, 2650–3000 m, 27.xi.1947 (fl), *Barkley, Garcia-Barriga & Vanegas* 17C814 (COL, US). Magdalena: Sierra Perijá, near Laguna el Juncos, above 'Africa', *c.* 2200 m, 16.xii.1944 (fl & fr), *Haught* 4503 (F, K). Meta: Páramo de Sumapaz, Hoya El Nevado, Laguna La Guitarra, 3460 m, 21.i.1972 (fr), *Cleef* 824 (COL, U). Norte de Santandér: Páramo del Hatico (between Toledo and Pamplona), *c.* 2900 m, 12–13.iii.1927 (fl), *Killip & Smith* 20662 (GH, NY). Putumayo: between Laguna La Cocha and Páramo de Tábano, *c.* 2800–3000 m, 1.i.1946 (fl), *Schultes & Villareal* 7834a (F). Santandér:* Bucaramanga (Cumbre to Cúcuta), 3300 m, v.1948 (fl),

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* Robust, large-flowered form (= *H. pseudobrathys* Turcz. sensu stricto).

Sandeman 6067 (BM, K); Páramo de Almorzadero, 3600–3800 m, 28.xi.1941 (fl), *Cuatrecasas* 13493 (COL, F, NY); limites entre los Departamentos Santandér y Boyacá, Corregimiento de Virolín, Finca 'La Sierra', 2500–2600 m, 18.vi.1976 (fl), *Lozano, Torres & Díaz* 2636 (COL). Tolima: 'Rosalito', near Páramo de Ruiz, 2800–3100 m, 15–17.xii.1917 (fl & fr), *Pennell* 2956 (F, GH, K, MO, NY).

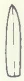
VENEZUELA. Mérida: Páramo de La Negra above Bailadores, 3100 m, 13.ii.1939 (fl), *Alston* 7024 (BM, S, U);* Páramo de Muruti, x.1865 (fl), *Moritz* 1165 (BM, GH, K, P, S); Páramo La Negra between Tovar and La Grita, 3000 m, 7.x.1965 (fl), *Breteler* 4619 (K, MO, NY, S, U, VEN). Táchira: Páramo Zumbador, 14 km S. of El Cobre, 2500 m, 31.iii.1974 (fl), *Gentry, Morillo & Morillo* 11068 (GH, MO, NY, VEN); Dtto. Uribante, a las cabeceras del río Uribante, 51 km al SW. de Pregonero, 2700–2900 m, 28.ix.1981 (fl), *Steyermark & Manara* 125420 (BM, VEN). Trujillo: Alredores de Guirigay, hacia Laguna La Parida, 3300 m, viii.1958 (fl), *Aristeguiéta & Medina* 3537 (NY, VEN).

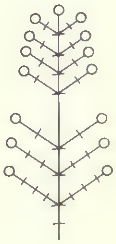
The variation in *H. juniperinum* is rather complex. Spach and Triana & Planchon distinguished a plant with larger, always 3-styled, sometimes solitary flowers and fruits and more appressed leaves (based on Kunth's *H. juniperinum*) from the typical small-flowered, spreading-leaved *H. brathys* Sm. (an illegitimate name) with 3–5 styles. Such a large-flowered plant can be recognized in western Venezuela (Trujillo, Mérida) and in isolated Colombian localities in Santandér, Boyacá, Cundinamarca, Antioquía, and Cauca, but it is linked to the typical '*H. brathys*' by intermediates. Indeed Kunth's type of *H. juniperinum* has flowers somewhat intermediate in size.

In Cauca there is a separate apparently continuous morphocline in which the styles are always three in number. This cline links the tall erect plants with crowded subappressed leaves and larger flowers (i.e. *H. juniperinum* sensu Spach and Triana & Planchon) with smaller, spreading to decumbent plants with stems rooting, longer internodes, smaller, closely appressed leaves, and smaller flowers. In its extreme expression, the latter form approaches *H. prostratum*, but can be distinguished from it by the larger leaves and flowers and the longer styles. Specimens exemplifying this end of the morphocline include *Idrobo, Pinto & Bischler* 3725 (COL, P), 3717 (COL) and *Barclay & Juajibioy* 5784 (COL, MO, NY), 5809 (COL, MO, NY), all from Valle de Los Papas, Los Andes, near Valencia.

42. **Hypericum prostratum** Cuatrec.

in *Brittonia* **11**: 166 (1959). Type: Colombia, Cundinamarca, Páramo de Sumapaz, 3800 m, 10.vi.1952 (fl), *Køie* 4621 (US!, holotype; C!, isotype).





Shrub or shrublet with shoots 0·1–0·3 m long, wiry, decumbent to prostrate and rooting at the base, the branches strict to spreading, lateral (irregularly pinnate), not pseudo-dichotomous. *Stem* orange-brown, 4-lined when young, soon 4-angled and ancipitous, eventually terete, cortex exfoliating irregularly; internodes 2–3 mm long. *Leaves* sessile, appressed at first, eventually spreading and twisting, not tetrastichous, deciduous above base without fading; lamina 2–5 × 0·5–0·8(–1·2) mm, linear to acicular, cucullate, midrib impressed beneath, margin broadly hyaline or golden, concolorous, not glaucous, subcoriaceous, apex acute, base parallel to cuneate, not broadening, pairs forming narrow interfoliar ridge; basal vein 1, unbranched; laminar glands ± dense and prominent above, sparse or not visible beneath. *Inflorescence* 1-flowered, terminal and sometimes on up to 6 short lateral shoots, without pseudo-dichotomous branches; pedicel almost absent or up to 2 mm long, not incrassate upwards; upper leaves not transitional. *Flowers* 4–8 ,m in diam., stellate to obconic. *Sepals* 4–5, 2–3·5 × 0·5–1 mm, lanceolate, acute, veins 5, unbranched, midrib not prominent; glands linear. *Petals* 4–5, bright yellow, 3–6 × 1·5–2 mm, 1·5–2 × sepals, oblong-obovate; apiculus acute; glands mostly linear. *Stamens* 7–10, longest 2·5–3·5 mm long, *c.* 0·65 × petals. *Ovary* 0·8–1 × 1 × 0·8 mm, subglobose; styles 3(4), 0·6–0·8 mm long, *c.* 0·8 × ovary, suberect; stigmas capitate. *Capsule* 2–2·5 × 1·5–2 mm, ellipsoid-subglobose to globose, shorter than to slightly exceeding sepals. *Seeds* 0·5–0·6 mm long, ecarinate; testa finely scalariform.

In open páramo, usually in damp areas; 3200–4200 m.

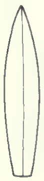
Colombia (Cundinamarca, Meta, Boyacá, Santandér). Map 17.

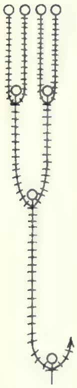
COLOMBIA. Boyacá: Páramo de Pisva, carretera Socha-La Punta, Km 61.5, 6 km al E. de Los Pinos, Alto de Granados, 3570 m, 11.vi.1972 (fl), *Cleef* 4374 (BM, COL, U); Páramo de La Rusia, NW.-N. de Duitama, Aislada, 3575 m, 6.xii.1972 (fl & fr), *Cleef* 6747 (COL, U); between Soatá and Cocuy, Páramo del Alto del Escobal, 3750 m, 8.ix.1938 (fl), *Cuatrecasas* 1224 (F). Cundinamarca: Bogotá-Usmé road, Páramo de Chisacá, between Kms 28 and 33, 3375–3450 m, 17.v.1979 (fl), *Luteyn* 7770 (BM, COL, MO, NY); Páramo de Cruz Verde, aprox. 5 km al ENE. de la Laguna El Verjón, 3360 m, 2.v.1972 (fl), *Cleef* 3371 (BM, COL, U); entre Cogua y San Cayetano, Laguna Verde y alredores, 3600 m, 12.xi.1972 (fl), *Cleef* 6260 (BM, COL, U). Meta: Páramo de Sumapaz, Hoya El Nevado, Laguna La Guitarra y alredores, 3460 m, 21.i.1972 (fl), *Cleef* 834 (BM, COL, U). Santandér: Páramo de Almorzadero, 3500–3700 m, 20.vii.1940 (fl), *Cuatrecasas & Garcia Barriga* 9998 (COL, US).

H. prostratum continues one of the reduction trends in *H. juniperinum*, differing from the decumbent Cauca plants in (for example) its prostrate habit, shorter and initially strongly appressed leaves, and smaller flowers and fruits. The direction of the trend, however, has been reversed, i.e. the westernmost specimens (from Cundinamarca and Meta) are nearest to the above-mentioned Cauca populations of *H. juniperinum* both morphologically and geographically.

43. **Hypericum parallelum** N. Robson, **sp. nov.**

H. magdalenico N. Robson affinis, sed foliis angustioribus glandulis prominentibus costa media haud ramosa, floribus minoribus stylis brevioribus sepalis glanduloso-punctatis, differt; a *H. pimelioidei* Planchon et Linden ex Triana et Planchon inter alia ramis strictissimis foliis angustioribus valde tetrastichis differt. Type: Colombia, Norte de Santandér/César, Linea divisoria entre los Deptos. Santandér del Norte y César, 20 km al sur de Abrego, Las Jurisdicciones (Cerro de Oroque), 3700–3960 m, 19–21.v.1969 (fl), *Garcia-Barriga & Jaramillo* 19749 (COL!, holotype).



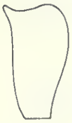


Shrub 0·3–0·4 m tall, erect, with branches very strict, crowded, parallel, pseudo-dichotomous, corymbiform. *Stems* orange-brown becoming blackish, 4-lined but not compressed when young, the subfoliar ridges broad, soon (?) terete, cortex exfoliating irregularly; internodes 1–1·5 mm long. *Leaves* sessile, densely imbricate, slightly outcurving, markedly tetrastichous, soon deciduous above base without fading; lamina 6–11 × 1·4–1·7 mm, narrowly elliptic, plane to incurved, cucullate, midrib slightly impressed beneath, margin narrowly hyaline, concolorous, papillose above, lucent beneath, not glaucous, coriaceous, apex acute, base narrowly cuneate, scarcely sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, apparently unbranched; laminar glands dense, ± prominent beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 2–2·5 mm long, slightly incrassate upwards; upper leaves not transitional. *Flowers c.* 10–12 mm in diam. (?), stellate (?). *Sepals* 6–7 × 1·5–2 mm, lanceolate, acute, veins 5, unbranched, the midrib not prominent; glands linear proximally, punctiform distally. *Petals* bright yellow, *c.* 9–10 × 2·5 mm, *c.* 1·3 × sepals, obovate; apiculus acute; glands linear, distally punctiform. *Stamens c.* 40–50, longest 4–5 mm long, *c.* 0·5 × petals. *Ovary c.* 2 × 1 mm, ellipsoid; styles 3, 2–2·5 mm long, *c.* 1–1·3 × ovary, spreading; stigmas broadly capitate. *Capsule* 5–5·5 × 2·5–3 mm, ellipsoid, acute, shorter than sepals. *Seeds* 0·8–0·9 mm long, ecarinate; testa scalariform.

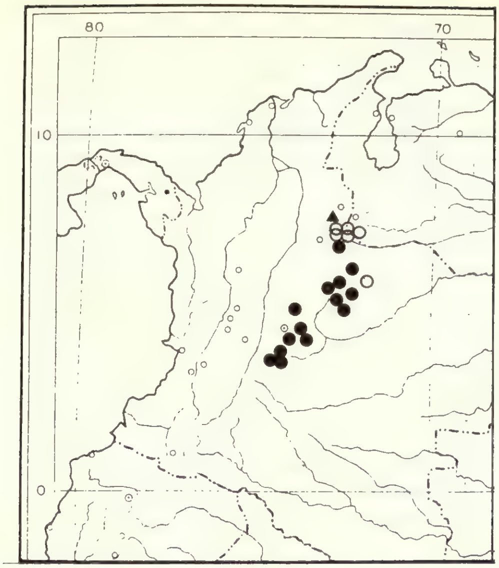
Páramo?; 3700–3960 m.

Colombia (N. de Santandér/César); known only from Las Jurisdicciones, Cerro de Oroque. Map 17.

COLOMBIA. N. de Santandér/César: Jurisdicciones, Cerro de Oroque, '3000–3700–3900 m', 22–27.vii.1974, *Garcia-Barriga & Jaramillo* 20659 (COL).



H. parallelum is clearly derived from the form of *H. magdalenicum* with small, coriaceous, densely imbricate leaves, but differs in the markedly tetrastichous, cucullate leaves with conspicuous gland dots and the very strict branching.



Map 17 42. *H. prostratum* ●; 43. *H. parallelum* ▲; 45. *H. lancifolium* ○.

44. **Hypericum marahuacanum** N. Robson, **sp. nov.**

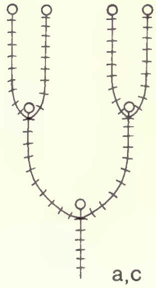
H. magdalenico N. Robson affinis, sed foliis minoribus acicularibus minus coriaceis, costa media haud ramosa, sepalis angustioribus stylis gracilioribus brevioribus, inter alia differt; a *H. lancifolio* Gleason foliis angustioribus lucentibus torquescentibus margine valde incurvatis differt. Type: Venezuela, Amazonas, Dept. Atabapo, Cerro Marahuaca, cumbre Seccion suroriental, 2685 m, 15.i.1981, *Maguire, Steyermark et al.* 65629 (VEN!, holotype; MO!, NY!, isotypes).

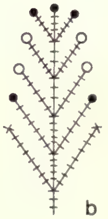
Icones: Fig. 12A–C.

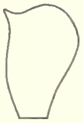
Shrub 0·3–1·5 m tall, erect, with branches strict to very strict, mostly pseudo-dichotomous to all lateral. *Stems* orange-brown, 4-angled and ancipitous when young, the subfoliar ridges broad, soon terete, cortex exfoliating irregularly; internodes 0·7–2 mm long. *Leaves* sessile, densely imbricate, erect to suberect, outcurving, twisting slightly or not, subtetrastichous to strictly tetrastichous, deciduous above base without fading; lamina 5–12 × 0·6–1 mm, linear, incurved, not cucullate, midrib impressed beneath, margin narrowly hyaline, concolorous, polished, not glaucous, coriaceous; apex acute, often slightly pungent, base parallel-sided, not sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, without reticulation; laminar glands in single irregular row, visible beneath or not. *Inflorescence* 1-flowered, sometimes with pseudo-dichotomous branches from node below; pedicel 2–3 mm long, not incrassate upwards; upper leaves not transitional. *Flowers* 10–15(–20?) mm in diam., stellate. *Sepals* 4–9 × 0·6 mm, narrowly lanceolate or narrowly oblong-lanceolate, acute, veins (3)5–9, unbranched, midrib impressed; glands linear, becoming prominent (sepals ribbed). *Petals* deep yellow to orange-yellow, 6–11 × 2·5–4 mm, *c.* 1·2–1·7 × sepals, obovate (?) to oblanceolate; apiculus sharply acute; glands linear, usually distally interrupted. *Stamens* 30–50, longest 3–9 mm long, 0·45–0·8 × petals. *Ovary* 1·2–3 × 1–1·5 mm, narrowly ellipsoid or narrowly ovoid-ellipsoid to ellipsoid-subglobose, acute to rostrate; styles 3(4), 2–5 mm long, 1·5–2 × ovary, outcurved to erect or ascending; stigmas narrow to narrowly capitate. *Capsule* 3·5–5 × 2–2·5 mm, narrowly ovoid to ovoid-ellipsoid, shorter than sepals. *Seeds* 1–1·2 mm long, ecarinate; testa finely scalariform.

Along shaded (?) streams, in swampy areas, and in drier places and on escarpment; 2500–2800 m.

Colombia (Boyacá), Venezuela (Mérida, Amazonas, Bolivar). Map 15 (p. 71).







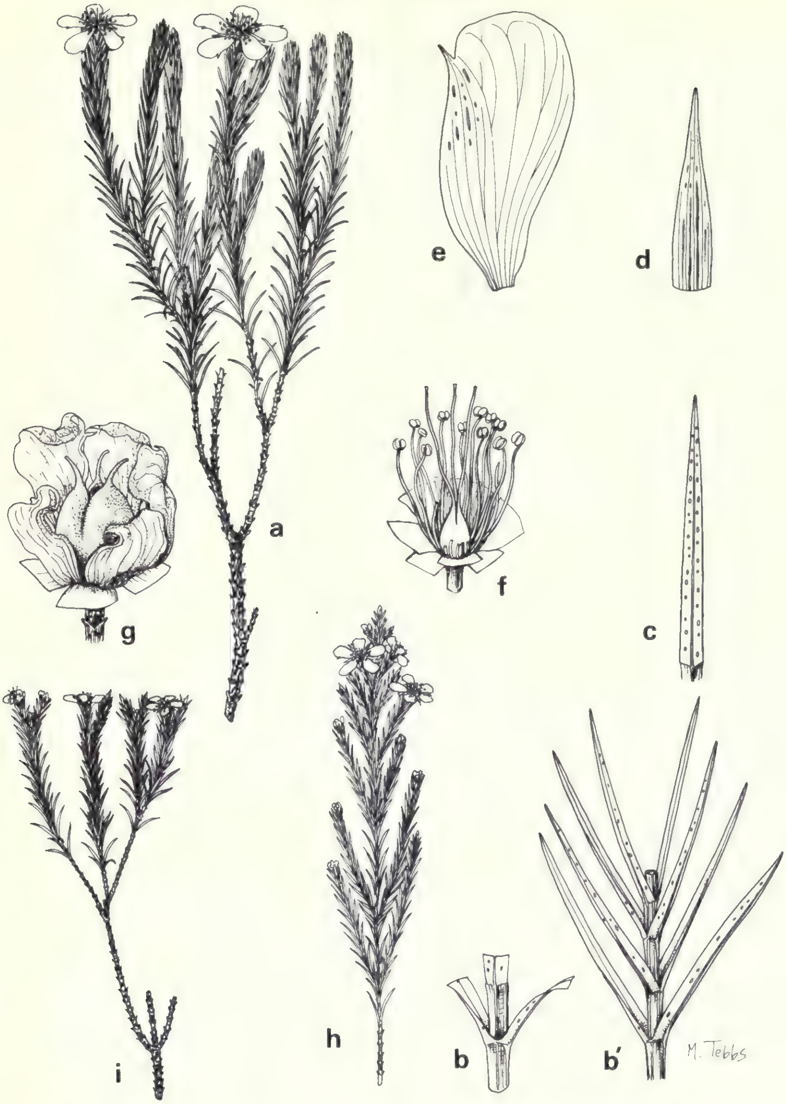


Fig. 12 *H. marahuacanum*. A. subsp. *marahuacanum*: (a) habit; (b, b′) stem with leaves (two aspects); (c) leaf; (d) sepal; (e) petal; (f) stamens (partly cut away) and ovary; (g) capsule. B. subsp. *strictissimum*: (h) habit. C. subsp. *chimantaicum*: (i) habit (a, h, i × ½; b–g × 3). A. *Maguire et al.* 65629; B. *Fosberg* 22209; C. *Huber & Steyermark* 7014.

H. marahuacanum sensu lato comprises four geographically isolated populations, which form three taxa. Although geographically separate, the morphological variation among them is almost continuous, and so the appropriate rank would seem to be subspecies.

Subsp. *marahuacanum* (Amazonas: Cerro de Marahuaca) has longer and usually broader sepals, longer petals, and nearly always longer styles than the other subspecies, the inflorescence branching is pseudo-dichotomous, and the ovary and capsule are acute and the stigmas narrow. Subsp. *chimantaicum* (Bolivar: Chimantá Massif, Roraima) has a rostrate ovary and capsule and broad to capitate stigmas, whereas in subsp. *strictissimum* (Mérida, Boyacá) the inflorescence branching is wholly lateral.

44a. **Hypericum marahuacanum** subsp. **marahuacanum**

Icon: Fig. 12A.

Branches strict, mostly paired and pseudo-dichotomous, rarely lateral. *Leaves* twisting slightly, strictly tetrastichous; lamina 7–10 × 1 mm, with glands visible beneath. *Inflorescence* branches pseudo-dichotomous; pedicel 2–3 mm long. *Flowers* 10–15(?–20) mm in diam. *Sepals* 7–9 × 1·3–2 mm, narrowly lanceolate or narrowly oblong-lanceolate, veins 5–9. *Petals* 10–11 × *c.*3 mm, *c.* 1·2–1·3 × sepals, obovate (?). *Stamens c.* 50, longest 7–9 mm long, 0·7–0·8 × petals. *Ovary* 2·5–3 × 1·3–5 mm, narrowly ellipsoid to narrowly ovoid-ellipsoid, acute; styles 4–5 mm long, 1·5–2 × ovary, outcurved; stigmas narrow to narrow capitate. *Capsule c.* 5 × 2 mm, narrowly ovoid.

Along shaded (?) steams and on escarpment; 25–2800 m.

Venezuela (Amazonas).
VENEZUELA. Amazonas: Departamento Atabapo, Cerro de Marahuaca, parte central de la Meseta S.-E., Quebrada Yekuana, afluente del río Negro, 2560 m, 10–12.x.1983, *Steyermark* 129511 (BM, VEN); Cerro de Marahuaca, al NE. de, y casi contigua con, Cerro Duida, *c.* 2750 m, 2 & 9.ii.1975, *Tillett, Colveé et al.* 752–335 (VEN).

Subsp. *marahuacanum,* apparently confined to the Cerro Marahuacana, is the only member of the genus recorded from that eminence. It is most closely related to the narrow-leaved form of *H. magdalenicum* from the Cerro de Perijá (Zulia), differing from it in the smaller, narrower leaves and the usually smaller flowers with narrower, ribbed sepals and shorter, more slender styles.

44b. **Hypericum marahuacanum** subsp. **strictissimum** N. Robson, **subsp. nov.**

a subsp. *marahuacano* ramulis plerumque lateralibus, foliis angustioribus, floribus minoribus, sepals 3–5-venatis, petalis quam sepalis 1·7plo longioribus, stylis 2·5–3 mm longis, inter alia differt. Type: Colombia, Boyacá, Socha, valley of Río Chicamocha, 2700–2750 m, 8.xi.1944 (fl), *Fosberg* 22209 (US!, holotype; NY!, P!, isotypes).

Icon: Fig. 12B.

Branches strict to very strict, some paired and pseudo-dichotomous or all lateral. *Leaves* twisting slightly or not, markedly tetrastichous; lamina 5–11 × 0·5–0·8 mm, with glands relatively few, mostly obscure. *Inflorescence* branches short, lateral, from up to *c.* 6 nodes below, sometimes with pseudo-dichotomous branches from uppermost node; pedicel *c.* 2 mm long. *Flowers c.* 10–12 mm in diam. *Sepals* 4–6 × 0·7–1·5 mm, narrowly lanceolate, veins (3)5. *Petals* 7–9 × 3–4 mm, *c.* 1·7 × sepals, obovate (?). *Stamens c.* 40, longest *c.* 3–4 mm long, *c.* 0·45 × petals. *Ovary* 1·2–1·5 × 1 mm, ellipsoid-subglobose; styles 2·5–3 mm long, *c.* 2 × ovary, suberect; stigmas scarcely enlarged. *Capsule* 4 × 2·5 mm, ovoid, acute, shorter than sepals.

Páramo and subpáramo, in dry stony places; 2700–3250 m.

Colombia (Boyacá), Venezuela (Mérida).
COLOMBIA. Boyacá: Carretera Socha-Los Pinos, Km 41, 2 km al N. del Alto Los Pinos y 4 km al ENE. de Socha, 2970 m, 22.v.1973 (fl), *Cleef* 9891 (COL, U); Páramo de Belén, *c.* 14 km N. of Belén, near 259 km marker (from Bogotá), *c.* 3250 m, 9.v.1959 (fl), *Barclay & Juajibioy* 7668 (NY).
VENEZUELA. Mérida: Páramo de Las Coloradas (entre Santa Cruz de Mora y El Molino), San Rafael, 2950–2950 m, 9.ii.1973 (fl), *Cuatrecasas, Ruiz-Terán & López-Figueiras* 28529 (BM, US); Sierra Nevada, i.1865 (fl), *Moritz* 1602 (BM).

Subsp. *strictissimum*, which comprises two geographically distinct populations, differs from subsp. *marahuacanum* in having narrower leaves, smaller flowers which terminate lateral branches as well as main ones, and shorter styles. When well developed (as in the type collection), the strict lateral branches gives subsp. *strictissimum* the appearance of some species of *Erica*.

44c. **Hypericum marahuacanum** subsp. **chimantaicum** N. Robson, **subsp. nov.**

a subsp. *marahuacano* caulibus gracilioribus, nonnihil magis divergentibus, foliis haud vel vix punctata, pedicellis longioribus, floribus minoribus interdum ramulis brevibus lateralibus terminantibus, stylis brevioribus anguste capitatis, capsula elliptica, differt. Type: Venezuela, Bolivar, Chimantá Massif, Central Seccion, E. branch of headwaters of Río Tirica, 2121 m, 12.ii.1955 (fr), *Steyermark & Wurdack* 7581 (VEN!, holotype; BM!, MO!, NY!, isotypes).

Icon: Fig. 12C.

Branches strict to ascending, paired and pseudo-dichotomous, rarely lateral. *Leaves* twisting slightly, subtetrastichous; lamina 8–12 × 0·6–0·8 mm, with glands few, obscure or apparently absent. *Inflorescence* sometimes with 2–4 short axillary shoots immediate below, pseudo-dichotomous; pedicel *c.* 3 mm long. *Flowers c.* 10 mm in diam. *Sepals* 4–6 × 0·6–1 mm, linear-lanceolate, acute, veins 5–7. *Petals* 6–8 × 2·5–3 mm, *c.* 1·5 × sepals, oblanceolate. *Stamens c.* 30?, longest *c.* 4–5 mm long, 0·6–0·7 × petals. *Ovary c.* 1·5–2 × 1 mm, ovoid-ellipsoid, rostrate; styles 2–3·5 m long, *c.* 1·5 × ovary, erect to ascending; stigmas narrowly capitate. *Capsule* 3·5–5 × 2–2·5 mm, ovoid-ellipsoid, acute to subrostrate.

In swampy open savanna; 2121–2200 m.

Venezuela (Bolivar: Macizo de Chimantá and Roraima).

VENEZUELA, Bolivar: Distrito Piar, Macizo de Chimantá, E., Apacará-tepui, sector Norte de Macizo, *c.* 2200 m, 30.i–1.ii.1983 (fl), *Steyermark, Huber & Carreño* 128351 (BM, VEN), *Huber & Steyermark* 7014 (BM, VEN); Cimo del Roraima, i.1977 (fl), *Delascio & Brewer* 4794 (VEN).

All the characters by which subsp. *chimantaicum* differs from subsp. *marahuacanum* are apomorphic (advanced). It is the easternmost taxon of those in the *H. magdalenicum* affinity and is as isolated as subsp. *marahuacanum*.

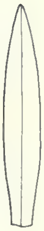
45. **Hypericum lancifolium** Gleason

in *Bull. Torrey bot. Club* **56**: 103 (clav.), 105 (1929). Type: Colombia, Santandér, vicinity of La Baja, 2200–2600 m, 14.i.1928 (fl), *Killip & Smith* 17138 (NY!, holotype; US!, isotype).

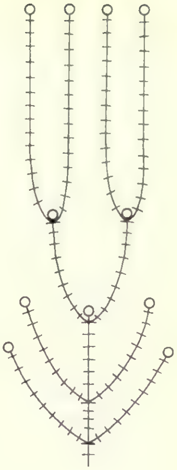
H. struthiolifolium sensu Knuth in *Reprium Spec. nov. Regni veg.*, Beih. **43**: 484 (1927) ['*struthiolaefolium*']; Cuatrec. in *Trab. Mus. nac. Cienc. nat. Jard. bot. Madrid* (Bot.) **33**: 83 (1936), non Juss. (1804).

H. weberbaueri sensu Gleason in *Bull. Torrey bot. Club* **56**: 102, 103, 105 (1929) pro parte, quoad specim. Colomb. cit., non R. Keller (1908).

H. lancioides sensu Steyerm. in *Fieldiana Bot.* **28**: 988 (1957).



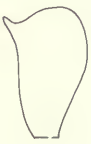
Shrub 0·2–1·5 m tall, erect, with branches strict, pseudo-dichotomous and sometimes lateral. *Stems* orange- to reddish-brown, 4-lined and ancipitous when young, the subfoliar ridges broad, soon terete, cortex exfoliating irregularly; internodes 1·5–3·5 mm long. *Leaves* sessile, subimbricate to narrowly spreading, ± tetrastichous, deciduous above base without fading; lamina 6–16 × 0·8–3 mm, narrowly oblong to very narrowly oblanceolate, plane to slightly incurved, not or scarcely cucullate, midrib not or scarcely impressed distally, margin narrowly hyaline, concolorous, undulate-papillose on both sides or sublucent beneath, sometimes glaucous, subcoriaceous; apex sharply acute, base angustate or parallel-sided, not sheathing, pairs united to form very narrow interfoliar ridge; basal vein 1, occasionally with 1–2 pairs of ascending lateral branches, not branching distally, not prominent beneath, tertiary reticulation absent; laminar glands dense, frequently prominent beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 2–4 mm long, rather slender; upper leaves not transitional. *Flowers* 10–20 mm in diam., stellate. *Sepals* 6–10 × 1·5–3 mm, narrowly to acuminate, incurved above, veins 3–5, unbranched or laterals branched, midrib not prominent; glands sometimes linear to striiform towards base, otherwise (or wholly) punctiform. *Petals* pale yellow, 8–12 × 3–5 mm, 1·1–1·3 × sepals, narrowly obovate; apiculus acute; glands punctiform. *Stamens* c. 30–70, longest 5–7 mm long, 0·5–0·75 × petals. *Ovary* 2·3 × 1–2 mm, ellipsoid; styles 3, 2–4 m long, 1–1·75 × ovary, outcurving; stigmas scarcely to broadly capitate. *Capsule* 4–7 × 2·5–3 mm, ellipsoid, acute, shorter than sepals. *Seeds* 0·7–0·8 mm long, ecarinate; testa finely scalariform-reticulate.



In páramo; *c.* 2600–3700 m.

Colombia (Boyacá, Santandér, N. de Santandér), Venezuela (Táchira, Apuré). Map 17 (p. 77).

COLOMBIA. Boyacá: Páramo de Chitá, cabeceras del río Casanare cerca la Lagunas de Ocubi, 3080 m, 23.v.1973, *Cleef* 9903 (U). Norte de Santandér: Pamplona, cerro al NE., 2700 m, 26.vii.1940, *Cuatrecasas & Garcia Barriga* 10218 (COL, F, US). Santandér: Páramo de la Puentas, above La Baja, 3500–3700 m, 25.i.1927, *Killip & Smith* 18187 (F, GH, K, NY, S, US).



VENEZUELA. Apuré: Páramo de Pata de Judío, en la frontera Colombo-Venezolana, 30 km al sur de San Vicente de la Revancha, SE. del Páramo de Tamá, 19.i.1968, *Steyermark & Dunsterville* 10122 (NY, VEN). Táchira: Páramo de Tamá, cerca de la frontera Colombo-Venezolana, 3000–3200 m, 20–23.v.1967, *Steyermark & Dunsterville* 98752 (VEN).

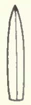
H. lancifolium is closest to the Duriamena population of *H. magdalenicum*, differing in the more slender stems, the narrower smaller, thinner leaves, and the smaller flowers with shorter styles. The typically plane narrow leaves are distinctive.

H. lancifolium has usually been labelled *H. weberbaueri*, but it differs from that Peruvian species (= *H. struthiolifolium*) in several respects, e.g. the plane (not incurved) leaves with prominent glands. These two species are not closely related.

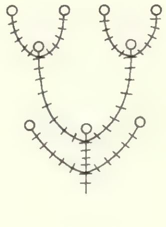
The Venezuelan population has shorter, narrower, outcurving leaves and smaller flowers with fewer stamens and shorter ovary, styles, and capsule. In addition, its height is usually less and its sepals usually narrower. The leaves are rarely plane as in *H. lancifolium*, always more or less incurved. It thus forms a transition to 46 *H. horizontale*.

46. **Hypericum horizontale** N. Robson, **sp. nov.**

H. lancifolio Gleason affinis, sed habitu prostato vel adscendenti, foliis secundis apice acicularibus, floribus minoribus, stigmatibus vix vel anguste capitatis, capsula minori, inter alia differt. Type: Colombia, Santandér, Páramo de Las Vegas, 3700–3800 m, 20–21.xii.1926, *Killip & Smith* 15617 (BM!, holotype; A!, GH!, K!, US!, isotypes).



Shrublet, up to *c.* 0·05 m tall, matted, with branches up to *c.* 0·3 m long, prostrate with apex ascending, rooting, branching mainly pseudo-dichotomous. *Stems* orange-brown, 4-angled and ancipitous when young, soon 2-lined, eventually terete, cortex exfoliating irregularly; internodes 1–3 mm long. *Leaves* sessile, not or scarcely imbricate, ascending to outcurving and secund, not tetrastichous, deciduous above base without fading; lamina 5–9 × 0·5–1·3 mm, linear, incurved-canaliculate, not cucullate, midrib impressed dorsally, margin narrowly hyaline, concolorous when mature, often red-tipped when young, sometimes sublucent, not glaucous, subcoriaceous; apex acicular, base parallel-sided, scarcely broadened, pairs forming narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense to sparse, visible on both sides. *Inflorescence* 1-flowered, terminal, and sometimes also on up to 9 short, paired lateral shoots, usually with pseudo-dichotomous branches from terminal node; pedical 1–2 mm long or almost absent; upper leaves not transitional. *Flowers* 8–12 mm in diam., stellate (? or shallowly obconic). *Sepals* (3·5–)4–6 – × 1–1·5 mm, narrowly oblong to narrowly or broadly lanceolate, distally incurved,



acute, margin hyaline, tip sometimes reddish, veins 5, unbranched, prominent; glands linear towards base, punctiform or absent distally. *Petals* bright (?) yellow, 5–7 × 2·5–3·5 mm, 1·1–1·4 × sepals, obovate; apiculus apiculate; glands striiform to punctiform. *Stamens c.* 25, longest 3–4 mm long, *c.* 0·6 × petals. *Ovary* 1·5–2 × 1–1·5 mm, ellipsoid-subglobose to globose; styles 3–4, 1·5–2·5 mm long, 1–1·3 × ovary, outcurving; stigma scarcely to narrowly capitate. *Capsule* 3–4 × 2–2·5 mm, cylindric-subglobose, obtuse to rounded, shorter than sepals. *Seeds* 0·6–0·8 mm long, ecarinate; testa finely scalariform.

In dry, open, sandy areas; 2800–4500 m.

Colombia (Norte de Santandér, Santandér). Map 18.

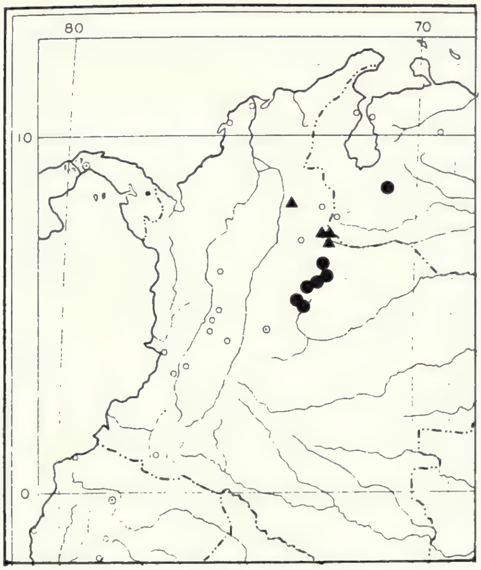
COLOMBIA. Norte de Santandér: Páramo de Santurbán, en route from Tona to Mutíscua, 4200–4500 m, 19.ii.1927 (fl & fr), *Killip & Smith* 19564 (BM, GH). Santandér: Páramo de Las Vetas, a 2 km del paraje de Berlin, *c.* 2800 m, 18.xii.1948 (fl & fr), *Molina & Barkley* 18S5410 (COL, F); idem, *c.* 3450 m, 3.vi.1960, *Barclay & Juajibioy* 10445 (MO, NY); Páramo de Almorzadero, 4200 m, 9.ix.1955 (fl), *Vareschi* 4070 (VEN p.p.); idem, auf der Passhöhe, 3850 m, 24.vii.1952, *Schneider* 1232 (S).

Although quite different in habit, *H. horizontale* is clearly related to the Venezuelan population of *H. lancifolium*. Its distinct distribution and morphological differences, taken together, indicate that it should be treated as a separate species.

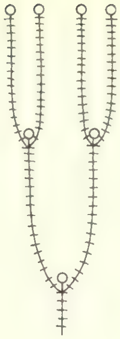
47. **Hypericum tetrastichum** Cuatrec.

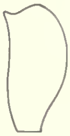
in *Ciencia Mex.* **23**: 144, f. 3A–G (1964). Type: Colombia, Santandér, Municipio de Onzaga, vereda de Chaguacá, alto de la Laguna de Los Bobos, en el filo divisorio Santandér-Boyacá, 3800 m, 7.viii.1958 (fl), *Jaramillo-Mejía, Hernández-Camacho & van der Hammen* 922 (US, holotype; COL, isotype); same data, *Jaramillo-Mejía, Hernández-Camacho & van der Hammen* 918 (COL!, topotype).

Shrub or shrublet 0·05–1 m tall, erect and ± densely caespitose, with branches strict, pseudo-dichotomous or (mostly) lateral. *Stems* orange-brown to blackish, 4-lined and compressed when young, the subfoliar ridges broad, soon or eventually terete, cortex exfoliating in strips or irregularly; internodes 0·5–6 mm long. *Leaves* sessile, erect, densely imbricate, markedly tetrastichous, the longer eventually spreading or



Map 18 46. *H. horizontale* ▲; 47. *H. tetrastichum* ●.





outcurving, not twisting, deciduous above the base without fading; lamina 6–13 × 0·6–1·5 mm, linear-acicular, carinate to incurved-canaliculate, cucullate or not, midrib prominent to impressed dorsally, margin narrowly (golden-) hyaline, sometimes red-tipped or red-tinged when young, otherwise concolorous, dull above, dull to sublucent beneath, not glaucous (at least when mature), subcoriaceous to coriaceous; apex acuminate to subacute, base broadened or parallel-sided, not sheathing, pairs united to form ± narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense to sparse or often absent beneath. *Inflorescence* 1-flowered, terminal, sometimes with short pseudo-dichotomous branches from node below; pedicel almost absent or up to 3 mm long, rather slender; upper leaves not transitional. *Flowers* 7–15 mm in diam., obconic. *Sepals* 4–8 × 1–2·2 mm, narrowly oblong to lanceolate, acutely acuminate to acute, incurved above, sometimes outcurving, often red-ripped or red-tinged, margin ± broadly hyaline, veins 3–5, unbranched, midrib or all becoming prominent (ribbed); glands linear, distally sometimes interrupted to punctiform. *Petals* bright yellow, 6–11 × 2·5–5·5 mm, 1·2–1·3 × sepals, oblong-obovate to obovate; apiculus acute to acuminate; glands interrupted to punctiform. *Stamens* 25–40, longest 3–5·5 mm long, 0·5 × petals. *Ovary* 1–2 × 0·7–1·3 mm, ellipsoid-subglobose to subglobose; styles 3(4), 1–2·5 mm long, 1–1·25 × ovary, outcurving to spreading; stigmas narrowly to broadly capitate. *Capsule* 3·5–5·5 × 2·5–3·5 mm, cylindric-ellipsoid to ellipsoid-subglobose, obtuse to rounded, shorter than sepals. *Seeds* 0·6–0·8 mm long, ecarinate; testa finely scalariform.

Wet or dry, often exposed areas in páramo and subpáramo; 2800–4160 m.

Colombia (Boyacá, Santandér, Venezuela (Mérida). Map 18.

COLOMBIA. Boyacá: Municipio Villa de Leyva, Parque Nacional Santuario de Iguaque, 3700 m, 20.vii.1979, *Melampy* 161 (COL); Municipio de Duitama, Páramo de La Rusia, 3400–3500 m, 28.xi.1978 (fl), *Díaz P.* 1243 (COL); Páramo de Guantiva, 3100 m, 26.vi.1964, *Espinal* 1733 (COL); páramos al NW. de Belén, vereda S. José de la Montaña, Alto de las Cruces y alredores, Cabeceras Q. El Toral, *c.* 3950 m, 24.ii.1972 (fl), *Cleef* 1736 (COL, U). Santandér: Páramo Ruso, 3150 m, 12.vii.1968 (fl), *Barclay & Mullen* 38C137 (COL).

VENEZUELA. Mérida: Sierra Nevada de Mérida, margen N. de la Laguna verde (al pie del Pico Humboldt), ± 4100 m, fl. 15–18.ii.1966, *Schulz, Rodriguez & Ramirez* 358 (U).

H. tetrastichum is closely related to *H. lancifolium* and *H. strictum*, differing essentially from the latter in its markedly tetrastichous foliage and in the length of the styles. The leaves appear pungent but may not be rigid when alive.

In some Boyacá localities, *H. tetrastichum* occurs in two apparently distinct forms: (i) leaves and flowers larger; leaves glandless beneath, apex acuminate-acicular (damp habitats); (ii) leaves and flowers smaller; leaves glandular beneath, apex acute (dry habitats). Until more information is available on the nature of this variation (genetical or environmental), it seems preferable not to give form (ii) any taxonomic recognition. Specimens of this form include:

Páramo de La Rusia, NW.-N. de Duitama, Laguna Negra, 3725 m, 14.xii.1972 (fl), *Cleef* 7208 (COL, U), 7208A (COL); Páramos al NW. de Belén, cabeceras Quebrada Minas, Hoya Laguna El Alcohol, 3900 m, 26.ii.1972 (fl), *Cleef* 1844 (U).

The drawing of the ovary accompanying the description of *H. tetrastichum* by Cuatrecasas depicts the styles as shorter than the ovary. However, my observations indicate that they are as long as or longer than the ovary, and suggest that the ovary depicted by Cuatrecasas had begun to enlarge after fertilization.

48. **Hypericum strictum** Kunth

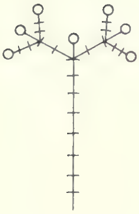
in Humboldt, Bonpland & Kunth, *Nova Gen. et Sp. Pl.* **5**: 190 (1822); Gleason in *Bull. Torrey bot. Club* **56**: 104 (1929) pro parte excl. vars. Type: Columbia, Cundinamarca, prope Santa Fé de Bogotá, 2880 m, 1805 (fl), *Humboldt & Bonpland* (P!, holotype; US!, photograph).

Shrub 0·2–1 m tall, erect, with branches strict, pseudo-dichotomous or mostly lateral, sometimes decumbent and rooting at the base. *Stems* orange-brown, 4-angled and ancipitous when young, then 2-lined, subquadrangular, eventually terete, cortex exfoliating in strips; internodes 1–7 mm long. *Leaves* sessile, imbricate, outcurving or spreading but not twisting, not or obscurely tetrastichous, deciduous above base without fading; lamina 5–13 × 5·6–1·3 mm, linear-acicular, incurved-canaliculate, cucullate or not, midrib impressed dorsally, margin narrowly hyaline, sometimes red-tipped when young, otherwise concolorous, dull to sublucent on both sides, glaucous when young, coriaceous to chartaceous; apex acute to subacuminate, base parallel-sided, pairs forming narrow interfoliar ridge; basal vein 1, unbranched; laminar glands absent or rarely sparse and visible beneath. *Inflorescence* 1-flowered, terminal and sometimes on short to long lateral branches from up to 5 nodes below (racemiform), sometimes with pseudo-dichotomous branches from node below; pedicel 2–5 mm long, rather slender to rather stout, not incrassate upwards; upper leaves not transitional. *Flowers c.* 12–20 mm in diam., stellate to obconic. *Sepals* 4·5–10 × 1–2 mm, lanceolate to narrowly oblong, acute to acutely acuminate, veins 3–5, unbranched, not or scarcely prominent but glands often ± depressed ('sepals ribbed'); margin ± broadly hyaline; glands linear, distally interrupted. *Petals* bright yellow, 6–11 × 3–7 mm, 1·1–1·3 × sepals, oblong-obovate to obovate; apiculus acute to apiculate; glands interrupted, distally subpunctiform. *Stamens* 35–50, longest 4–7 mm long, *c.* 0·65 × petals. *Ovary* 1·3–2 × 1–1·5 mm, ellipsoid to ovoid-ellipsoid or subglobose; styles 3, 2–3 mm long, 1–1·5 × ovary, ascending; stigmas narrowly to broadly capitate. *Capsule* 4–6 × 2·5–3·5 mm, ellipsoid, acute to obtuse, shorter than sepals. *Seeds* 0·6–0·8 mm long, ecarinate; testa finely scalariform-reticulate.

In exposed areas in páramo and subpáramo, and open grassland; 2120–4000 m.

Colombia (Santandér, Boyacá, Cundinamarca, Meta). Map 19.

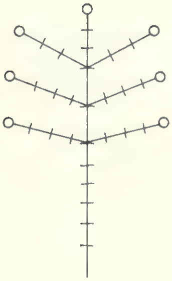
H. strictum is closely related to *H. tetrastichum*, differing from it in the leaves, which soon cease to be clearly tetrastichous as a result of stem internode elongation and leaf outcurving. In addition the leaf apex is never so sharply acuminate as it is in the longer-leaved form of *H. tetrastichum*, and the sepal form and glands are distinct. *H. strictum* also has a different, though overlapping distribution, being centred in Cundinamarca and showing trends north-east and south-west from there along the Cordillera Oriental. Some Boyacá specimens verge toward *H. tetrastichum* morphologically; others are quite distinct from that species and, indeed, form a derivative subspecies of *H. strictum*.



48a. **H. strictum** subsp. **strictum**

H. struthiolifolium var. *strictum* (Kunth) Choisy in DC., *Prodr. syst. nat. regni veg.* **1**: 553 (1824) ['*struthiolaefolium*']; Weddell, *Chloris Andina* **2**: 271 (1857); Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 294 (1862).

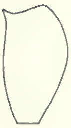
Leaves 8–13 mm long, outcurving, with apex subacuminate to acute, not cucullate, rarely red-tipped when young, dull, usually eglandular beneath. *Stems* simple, usually erect. *Sepals* 5–10 × 1·3–2 mm, lanceolate, acutely acuminate to acute, usually outcurving, rarely red-tipped; veins 5; glands adjacent to midrib often depressed. *Petals* 8–11 mm long. *Stamens c.* 50, longest 4–7 mm long. *Ovary* 1·5–2 mm long, ellipsoid to ovoid-ellipsoid. *Seeds* 0·7–0·8 mm long.

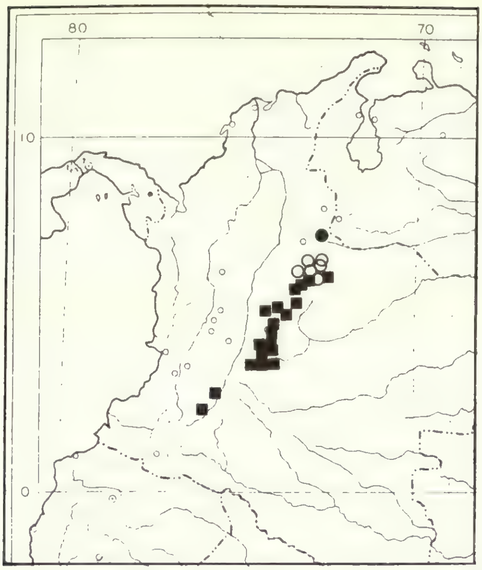


In dry rocky páramo and open grassland.

Colombia (Boyacá, Cundinamarca, Meta).

COLOMBIA. Boyacá: Río Grande, 2 km N. of Cómbita, 3445 m, 1.ix.1944 (fl), *St. John* 20695 (NY, US); NW. of Belén, Hoya El Pulpito, 2 km ESE. of Laguna Grande, 3805 m, 6.v.1973 (fl), *Cleef* 9775 B (COL). Cundinamarca: Represa del Neusa, 3350 m, 22.vi.1957 (fl), *Barclay* 4157 (COL); Zipaquirá – Pacho, Páramo Alto, 11.iii.1951 (fl), *Romero-Castañeda* 2282 (COL, F); Páramo de La Calera, 3000–3300 m, 25.ii.1950 (fl & fr), *Philipson, Idrobo & Fernandez* 2440 (BM, COL, F); Bogotá, páramo above El Chicó, 3150–3300 m, 11.vii.1943 (fl), *Fosberg &*





Map 19 48. *H. strictum*: a. subsp. *strictum* ■, b. subsp. *compactum* ('gracile' form) ○, ('compactum' form) ●.

Villareal 20585 (COL, NY, US). Meta: Páramo de Sumapaz, Cerro Nevado del Sumapaz, 3720 m, 31.i.1972 (fl), *Cleef* 1535 (U).

H. strictum subsp. *strictum* can be recognized by its dull, outcurving, usually apparently eglandular leaves and the lanceolate sepals that are not or scarcely ribbed but often have the two linear glands on either side of the midrib impressed.

48b. **H. strictum** subsp. **compactum** (Triana & Planchon) N. Robson, **comb. et stat. nov.**

H. pseudobrathys Turcz. in *Bull. Soc. Nat. Moscou* **31** (1): 387 (1858) ['*pseudobrathys*'] pro parte, quoad spec. *Funck & Schlim* 1279, *Linden* 1313.

H. struthiolifolium [var.] γ *compactum* Triana & Planchon [in Weddell, *Chloris Andina* **2**: 271 (1857) ['*struthiolaefolium*', '*confertum*'], nomen] in *Annls Sci. nat.* (Bot.) IV, **18**: 294 (1862). Type: Colombia, Santandér, prov. de Pamplona, San Urban, 2570 m, 1846 (fl), *Funck & Schlim* 1279 (COL?, holotype; BM!, P!, isotypes).

H. brathys sensu Trev., *Hyper. Animad.*: 15 (1861) pro parte, quoad spec. *Linden* 1313.

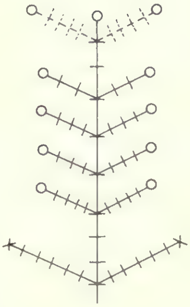
H. struthiolifolium [var.] ε *gracile* Triana & Planchon [in Weddell, *Chloris Andina* **2**: 271 (1857), nomen] in *Annls Sci. nat.* (Bot.) IV, **18**: 294. (1862), ['*struthiolaefolium*'] nom. illegit., pro parte, quoad spec. *Linden* 1313.

H. laricifolium var. *glaucum* R. Keller in *Bull. Herb. Boissier* II, **8**: 182 (1908). Type: Colombia, Boyacá, prov. Tunja, Páramo de Coati, près de Serinsa, 2870 m, 1842–1843 (fl), *Linden* 1313 (W!, holotype; GH!, KW!, P!, W!, isotypes).

H. strictum var. *compactum* (Triana & Planchon) Gleason in *Bull. Torrey bot. Club* **56**: 104 (1929).

H. graciliforme N. Robson in Cleef, *Veg. Páram. Colomb. Cord. Or.*: 304 (1981), nomen.

Stems usually branched from the base, ± ascending. *Leaves* 5–7(–8) mm long, outcurving or spreading with apex subacute, ± cucullate, markedly red-tipped or -tinged when young, dull to sublucent, often glandular beneath. *Sepals* 4·5–5·5(–6) × 1–1·2(–1·5) mm, triangular-lanceolate to narrowly oblong, acute to subacute, not outcurving, red-tipped or -tinged; veins 3(–5), all ± impressed. *Petals* 6–8(–10) m



long. *Stamens* 30–40, longest 4–5 mm long. *Ovary* 1·3–2 mm long, ellipsoid-subglobose to subglobose. *Seeds* 0·6–0·7 mm long.

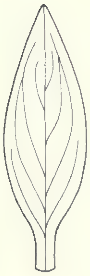
Wet areas in páramo and subpáramo, often with *Espeletia* spp.

Colombia (Boyacá, Santandér).

COLOMBIA. Boyacá: Páramo de Santa Rosa, entre Santa Rosa de Viterbo y Cerinza, 2800 m, 17.vii.1940 (fr), *Cuatrecasas & Garcia Barriga*. 9721 (COL, K, NY, P); Páramo de Guantiva, Alto de Canutos, 3200–3400 m, 3.x.1940 (fl & fr), *Cuatrecasas* 10329 (COL, F, US). Páramo de La Rusia, NW.-N. de Duitama, Aislada, 3490 m, 8.xii.1972 (fl & fr), *Cleef* 6835 (U). Santandér: Páramo de Santurbán, near Vetas, 3950–4160 m, 17.i.1927 (fl), *Killip & Smith* 17567 (A, BM, K, US).

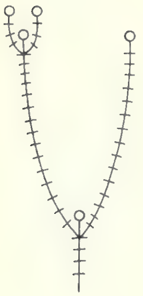
Subsp. *compactum* differs from subsp. *strictum* in the subacute to acute, cucullate, usually glandular leaves and the markedly ribbed sepals, both leaves and sepals being frequently red-tipped or red-tinged when young. It comprises two forms, which are geographically almost distinct and differ mainly in habit. The form in Santandér ('var. *compactum*'), which is confined to the Páramo de Santurbán, has relatively stout stems with crowded branches that at higher altitudes (3570–4160 m) form a compact, caespitose clump or prostrate mat. The leaves are relatively stout, often broader towards the tip, and remain erect and distinctly tetrastichous, and the sepals are rarely red-tipped. Most of the Boyacá and Cundinamarca plants have taller, relatively slender, more loosely branched stems forming lax bushes ('var. *gracile*'), and the sepals are usually red with a hyaline margin.

The '*gracile*' form has been confused with the superficially similar Peruvian – Ecuadorian *H. aciculare*, from which it differs by its oblong (not lanceolate) sepals, which (like the leaves) are nearly always tipped or tinged reddish, become markedly ribbed and have relatively broad hyaline margins. In addition, the styles are capitate and the seeds only about half as long, and the leaves become outcurved, not twisted.

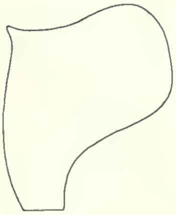


49. **Hypericum jaramilloi** N. Robson, **sp. nov.**

H. caracasano Willd. affinis, sed foliis et floribus maioribus, sepalis longioribus, petalis latioribus, staminibus numerosioribus, stylis longioribus, stigmatibus angustioribus, differt. Type: Colombia, linea divisoria entre los Deptos. Santandér del Norte y César, entre Abrego y Las Jurisdicciones (Cerro de Oroque), 3440–3750 m, 19–21.v.1969 (fl), *Garcia-Barriga & Jaramillo Meija* 19810 (COL!, holotype).



Shrub 1–1·5 m tall, erect, with branches strict, pseudo-dichotomous or occasionally lateral. *Stems* orange-brown, 4-angled when young, the subfoliar ridges broad, eventually terete, cortex exfoliating in strips; internodes 3–9 mm long. *Leaves* with ± distinct petiole 1–3 mm long, ± densely imbricate at first, soon outcurving then usually widely spreading above petiole, subtetrastichous, deciduous above petiole without fading; lamina 9–15)–20) × 2·5–5(–6·5) mm, usually narrowly elliptic, plane to subincurved, not cucullate, midrib not prominent beneath, margin not distinct, concolorous, glaucous, coriaceous; apex acute, base angustate, incurved but not sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, with 3–4 pairs of ascending main laterals, obscurely branching distally, tertiary reticulation absent; laminar glands dense, sometimes obscure. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 5–13 mm long, slightly incrassate distally; upper leaves broader but not transitional. *Flowers* 25–30 mm in diam., stellate. *Sepals* 9–14 × 3–6 mm, broadly to narrowly obovate or oblanceolate to elliptic-oblong or narrowly obovate or oblanceolate to elliptic-oblong or narrowly elliptic, acute to subacuminate, veins 5–7, unbranched, with midrib not or slightly prominent; glands linear to punctiform. *Petals* bright yellow, 12–17 × 6–10 mm, 1·2–1·5 × sepals, obovate; apiculus acute; glands linear, distally punctiform. *Stamens c.* 70–80, longest 6–8 mm, *c.* 0·5 × petals. *Ovary* 3·5–4 × 2 mm, cylindric-ellipsoid; styles 3, 6–7 mm long, *c.* 1·5 × ovary, distally outcurved; stigmas scarcely capitate. *Capsule c.* 8 × 4–5 mm, cylindric-ellipsoid to cylindric, shorter than sepals. *Seeds* not seen.



Páramo; 2600–3960 m.

Costa Rica (Limón), Colombia (Magdalena, César/Norte de Santandér). Map 20.

COSTA RICA. Limón: Cordillera de Talamanca, Cerro Kámuk massif, between Cerro Dudu and Cerro Apri, 2900–3100 m, 23 & 26.iii.1984 (fl), *Davidse, Herrera & Warner* 25880 (MO).

COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, transecto del Alto Río Buritaca, 2900 m, 5.viii.1977 (fl), *Jaramillo et al.* 5371 (BM, COL); loc. cit., 3300 m, 9.viii.1977 (fl), *Jaramillo et al.* 5454 (COL, U). César/Norte de Santandér: Cerro de Oroque, Las Jurisdicciones, 3700–3900 m, 22–27.vii.1974 (fl), *Garcia Barriga & Jaramillo* 20598 (COL); Cerro de Oroque, 20 km al S. de Abrego, 3700–3960 m, 19–21.vii.1974 (fl), *Garcia Barriga & Jaramillo* 19728 (COL).

H. jaramilloi is related on the one hand to *H. pimeleoides* and on the other to both *H. cardonae* and *H. ruscoides*. Its area of distribution overlaps that of *H. pimeleoides* in the Cerro de Oroque, where it can be distinguished by (i) the narrower spreading leaves with narrow (and usually longer) petioles and pinnate venation and (ii) the narrower sepals. From both *H. cardonae* and *H. ruscoides* it can be distinguished by size of parts (it resembles a larger, more primitive version of the latter), in particular by the longer styles.

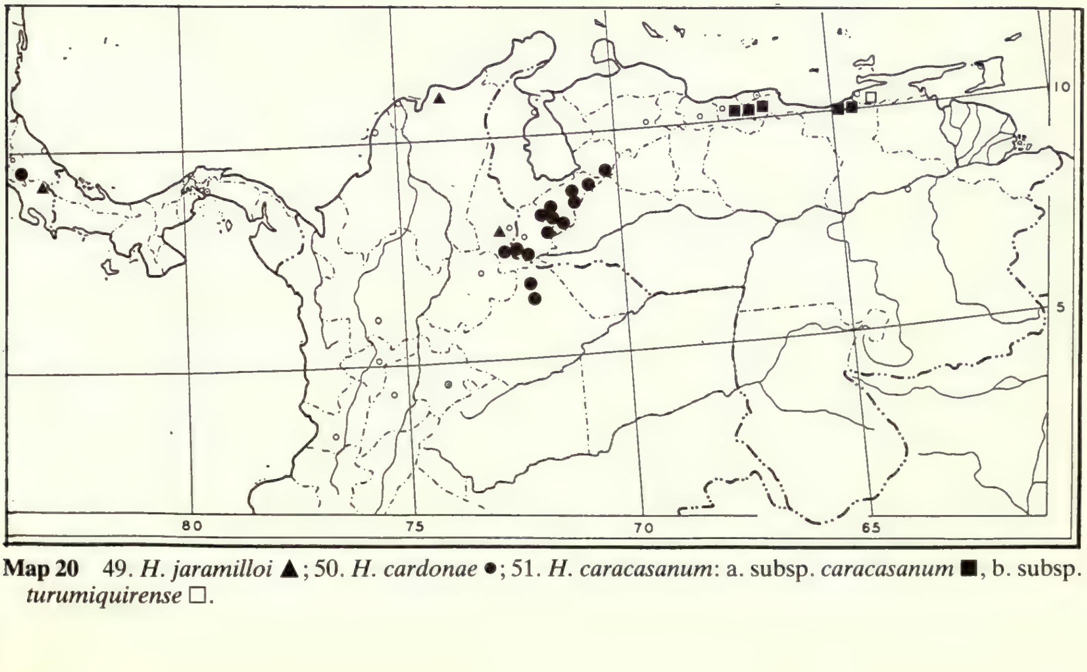
50. **Hypericum cardonae** Cuatrec.

in *Revta Acad. colomb. Cienc. exact. fis. nat.* **6**: 62 (1944), in *Trab. Com. Bot. etc. Colomb.*: 36 (1944). Type: Venezuela, Táchira, Páramo de Tamá, 3100–3300 m, vii.1939 (fl), *Cardona* 303 (VEN!, holotype; F!, isotype).

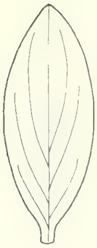
H. caracasanum sensu Turcz. in *Bull. Soc. Nat. Moscou* **31** (1): 389 (1858); Knuth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 483 (1927) pro parte, quoad spec. merid., et auct. plur.

H. caracasanum subsp. *cardonae* (Cuatrec.) N. Robson in Cleef, *Veg. Páram. Colomb. Cord. Or.*: 305 (1981), comb. illegit. sine basionym.

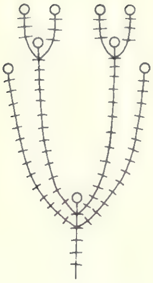
Shrub or shrublet 0·2–1 m tall, erect or rarely decumbent and rooting at the base, with branches strict, pseudo-dichotomous or lateral. *Stems* yellow- to orange-brown, 4-lined and ancipitous when young, the subfoliar ridges broad, soon terete, cortex exfoliating in strips; internodes 3–7 mm long. *Leaves* with petiole 1–2·5 mm long,



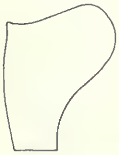
Map 20 49. *H. jaramilloi* ▲; 50. *H. cardonae* ●; 51. *H. caracasanum*: a. subsp. *caracasanum* ■, b. subsp. *turumiquirense* □.



persistently imbricate-tetrastichous to widely spreading from above petiole, deciduous above petiole without fading; lamina 7–15 × 2·5–7 mm, broadly to narrowly elliptic or narrowly oblong, plane to incurved or subconduplicate, not cucullate, midrib not or slightly prominent beneath, margin plane to incrassate, concolorous, often glaucous to blue-green, coriaceous; apex acute to subrounded, base angustate to cuneate, the petioles not sheathing but united to form narrow interfoliar ridge; basal vein 1, with (1–)2–3 pairs of ascending lateral branches (often obscure), rarely visibly branching, not impressed beneath, tertiary reticulation not visible; laminar glands dense, visible beneath or not. *Inflorescence* 1-flowered, sometimes with several flowering branches clustered, with pseudo-dichotomous branches from one or two nodes below; pedicel 4–6 mm long, not incrassate distally; upper leaves not transitional. *Flowers* 12–18 mm in diam., stellate or obconic. *Sepals* 6–12 × 2–4 mm, broadly to narrowly elliptic or oblong-elliptic to oblong-spathulate, acute to subacute; veins 5–7, sometimes branched distally, with midrib not or slightly prominent; glands mostly linear, distally punctiform. *Petals* bright yellow to orange-yellow, 8–11 × 3–6 mm, *c.* 1·3 × sepals, oblanceolate to obovate; apiculus acute; glands mostly linear, distally punctiform. *Stamens* 40–60, longest 4–7 mm long, *c.* 0·5 × petals. *Ovary* 2·5–3 × 1·5–2 mm, ovoid-ellipsoid to ellipsoid-subglobose; styles 3, 3–5 mm long, 1–1·6 × ovary, divergent to suberect; stigmas broadly capitate. *Capsule* 4–8 × 2–4 mm, cylindric-ellipsoid, equalling or shorter than sepals. *Seeds* 1–1·2 mm long, ecarinate; testa finely scalariform.



In humid (shaded or open) places in the páramo; 2500–4160 m.



Costa Rica (Cartago, San José), Venezuela (Trujillo, Mérida, Táchira, Apuré), Colombia (Norte de Santandér, Santandér, Boyacá, Arauca). Map 20 (p. 87).

COSTA RICA. Cartago: Cordillera de Talamanca, 'Cerro de la Muerte', Pan-American Highway 5 km above Millsville (8 km above Nivel), 3400–3300 m, vii.1949 (fl), *Holm & Iltis* 454 (F, GH, K, MO, NY, P, U). San José: Valle de los Conejos (upper Río Talari) and trails to Cerro Cirripó and Valle de los Lagos, 3400–3820 m, 22.viii.1971 (fl), *Burger* 8281 (BM, DUKE, F).

COLOMBIA. Arauca: Sierra Nevada del Cocuy, Quebrada El Playón, 3350 m, 13.iii.1973 (fl), *Cleef* 9182D (COL). Boyacá: paramos al NW. de Belén, cabeceras Quebrada Minas, Hoya Laguna El Alcohol, 3800 m, 26.ii.1972 (fl), *Cleef* 1870 (U); Cocuy Mts, valley of Quebrada Playitas above Guican, 3800 m, 24.vi.1984 (fl), *Wood* 4453 (K). Norte de Santandér: Páramo de Tamá, alredores de la Cueva, 3000–3200 m, 28.x.1941 (fl), *Cuatrecasas, Schultes & Smith* 12691 (COL). Santandér: Páramo de Santurbán near Vetas, 3950–4160 m, 17.i.1927 (fl), *Killip & Smith* 21167 (NY).

VENEZUELA. Apuré: Páramo de Pata de Judío, 30 km al S. de San Vicente de Revancha, 3000–3200 m, 19.i.1968 (fl), *Steyermark & Dunsterville* 101140 (NY, VEN). Mérida: Páramo de Los Leones (La Lagunita, La Cañada Grande), W. of Mucurubá, 3500 m, 31.v.1930 (fl & fr), *Gehringer* 138 (F, GH, NY, VEN); Villa de Caracas, Las Lagunetas, xi. (fl & fr), *Moritz* 1167 (BM, GH, K, KW, S). Táchira: Páramo El Batallón, 3200–3600 m, 3.x.1956 (fl), *Vareschi* 5491 (VEN); Hoya del Río Táchira, cabeceras de la Quebrada de El Reposo, 2800–3000 m, 16.i.1973 (fr), *Cuatrecasas, Ruiz-Terán & López-Figueras* 28330 (BM, US); Páramo de Tamá, cerca la frontera Colombo-Venezolana, 3000–3200 m, 20–23.v.1967 (fl), *Steyermark & Dunsterville* 98735 (VEN).

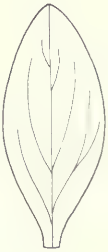
Some forms of *H. cardonae* from Mérida are rather similar to *H. caracasanum*, but the capitate stigma and the thicker, glaucous leaves with glands obscure or invisible will easily distinguish it. There is a southward reduction trend in habit and in leaf shape, plants from the Páramo de Tamá to Belén being dwarfer (almost suffruticose) and having smaller leaves, with thickened margin, obtuse to subrounded apex, and a longer thinner petiole. The Costa Rican population is more similar to plants from Mérida, but shows a similar reduction tendency to that of the southern plants.

For differences between *H. cardonae* and *H. caracasanum*, see the description of the latter species. The reduced form of *H. pimeleoides* can be distinguished from that of *H. cardonae* by the broader leaves with flabellate venation visible beneath.

51. **Hypericum caracasanum** Willd.

Sp. Pl. **3**: 1458 (1802); Choisy, *Prodr. monogr. fam. Hypéric.* 58 (1821); Kunth in Humboldt, Bonpland & Kunth, *Nova Gen. et Spec. Pl.* **5**: 186 (1822); Choisy in DC., *Prodr. syst. nat. regni veg.* **1**: 554 (1824); Turcz. in *Bull. Soc. Nat. Moscou* **31** (1): 389 (1858); R. Keller in *Bull. Herb. Boissier* II, **8**: 177 (1908); in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Knuth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 483 (1927) pro parte, excl. spec. merid.; Gleason in *Bull. Torrey bot. Club* **56**: 103. (1929); Steyerm. & Huber, *Fl. Avila*: 493, t. 152B (1978). Type: Venezuela, Distrito Federal, Silla de Caracas, i.1800 (fl), *Humboldt & Bonpland* 649 (B, holotype, F!, US!, photographs; P!, isotype).

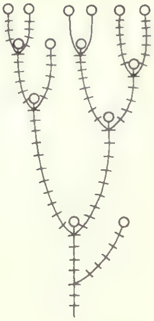
Shrub or shrublet 0·5–1·8 m tall, erect, with branches strict, pseudo-dichotomous or lateral. *Stems* yellow- to orange-brown, 4–6-lined and compressed when young, the subfoliar ridges broad, soon or eventually terete, cortex exfoliating in strips; internodes 1–4 mm long. *Leaves* subsessile to broadly or narrowly petiolate with petiole up to 1·5 mm long, ± densely imbricate, tetrastichous, ascending to outcurving, deciduous above petiole without fading; lamina 5–14(–17) × 2–7 mm, ± narrowly elliptic or ovate-elliptic to oblong, plane to incurved or slightly cucullate, midrib slightly prominent to impressed beneath, margin plane to recurved or slightly incrassate, paler beneath or concolorous or with margin pinkish, not glaucous, coriaceous; apex acute to subacute, base angustate, the petioles not or scarcely sheathing but united to form narrow interfoliar ridge; basal vein 1, with 1–3(4) pairs of ascending lateral branches, not visibly branching, not impressed beneath, tertiary reticulation not visible; laminar glands dense, usually visible beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 2·5–5·5 mm long, not or scarcely incrassate upwards; upper leaves not transitional. *Flowers* 12–20 mm in diam., stellate. *Sepals* 5–11 × 2–4·5 mm, broadly or narrowly elliptic or oblong-elliptic to obovate-spathulate or oblanceolate, acute to subacute; veins 3–7, sometimes branched distally, with midrib slightly prominent; glands linear, distally punctiform. *Petals* bright? to deep yellow, 8–13 × 3·5–6 mm, 1·4–2 × petals, oblanceolate; apiculus acute; glands mostly linear, distally interrupted to punctiform. *Stamens c.* 50–70, longest *c.* 4–7 mm long, *c.* 0·5 × petals. *Ovary* 2–3·5 × 2 mm, ovoid-ellipsoid; styles 3, 4–5 mm long, *c.* 1·5–2·5 × ovary, diverging and sometimes incurved; stigmas narrow or clavate. *Capsule* (5)6–8 × (2)3–4 mm, cylindric-ellipsoid, equalling sepals. *Seeds c.* 1·2 mm long, ecarinate; testa finely scalariform.



In humid or shaded habitats in the páramo and subpáramo; (1600) 2000–2765 m.

Venezuela (Distrito Federal, Miranda, Aragua, Anzoátegui, Sucre). Map 20 (p. 87).

H. caracasanum and *H. cardonae* are vicarious species which differ in leaf shape, thickness and glandularity, and in stigma shape, but *H. caracasanum* is more restricted in morphological variation and distribution than is its vicariad. In *H. caracasanum* the leaf glands are always visible and the stigma is not or scarcely enlarged. It appears to be directly related to *H. jaramilloi*.



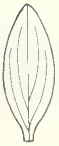
The extreme easternmost population of *H. caracasanum*, in the Cerro de Turumiquire (Sucre), has smaller, more crowded leaves and somewhat smaller flowers than the rest of the species, thus showing a trend in morphology as well as geography towards *H. ekmanii* from Hispaniola. The variation between the Sucre population and the rest is apparently almost continuous, and therefore subspecies is the appropriate rank for the two populations.

51a. **H. caracasanum** subsp. **caracasanum**

Brathys caracasana (Willd.) Spach, *Hist. nat. vég.* Phan. **5**: 448 (1836) in *Annls Sci. nat.* (Bot.) II, **5**: 366 (1836).

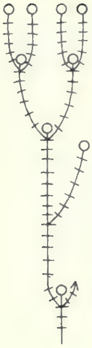
Icones: Steyerm. & Huber, *Fl. Avila*: t. 152B (1978); Fig. 13A.

Shrub or shrublet 0·5–1 m tall. *Stem internodes* 2–4 mm long. *Leaves* subsessile or with petiole up to 1·5 mm long; lamina 7–14(–17) × (2–)3·5–7 mm, narrowly elliptic to oblong. *Pedicels* 4·5–5·5 mm long. *Flowers* 15–20 mm in diam. *Sepals* 8–11 × 2–4·5 mm, broadly or narrowly elliptic or oblong-elliptic to obovate-spathulate, veins 5–7. *Petals* bright? yellow, 11–13 × 5–6 mm, *c.* 1·4 × sepals. *Ovary* 2–3 × 1·5–2 mm; styles 4–4·5 mm long, *c.* 1·5–2 × ovary.



In humid habitats in the páramo; (1600)2000–2763 m.

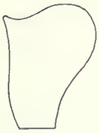
Venezuela (Distrito Federal, Miranda, Aragua, Anzoátegui).
VENEZUELA. Anzoátegui: Río Mantiales E. of Bergantía, Cerro Peonia above Santa Cruz, 2350 m, 21.iii.1945 (fl), *Steyermark* 61667 (F, NY, S, VEN). Aragua: prope Colonia Tovar, 1854–1855 (fl), *Fendler* 40 (GH, K, MO, P). Distrito Federal: Silla de Caracas, Cordillera de Avila, between Los Venados and Pico Oriental, 1675–2640 m, 27–28.ii.1944 (st), *Steyermark* 55644 (F, NY). Miranda: Pico de Naiguatá, above Los Chorros, 2200–2675 m, 16–17.vi.1945 (fl), *Steyermark* 62943 (F, NY).



51b. **H. caracasanum** subsp. **turumiquirense** (Steyerm.) N. Robson, **stat. nov.**

H. caracasanum var. *turumiquirense* Steyerm. in *Fieldiana Bot.* **28**: 393 (1952). Type: Venezuela, Sucre, Cerro Turumiquire, north-facing slopes, 2360–2500 m, 6.v.1945 (fl), *Steyermark* 62579 (F!, holotype; NY!, US!, isotypes).

Shrub 0·8–1·8 m tall. *Stem internodes* 1–2 mm long. *Leaves* with petiole 1–1·5 mm long; lamina 5–8 × 2–3·5 mm, ovate-elliptic to elliptic. *Pedicels* 2·5–3 mm long. *Flowers* 12–18 mm in diam. *Sepals* 5–6 × 2–3 mm, obovate-oblong to oblanceolate-spathulate, veins 3–5. *Petals* deep yellow, 8–12 × 3·5–4·5 mm, 1·5–2 × sepals. *Ovary c.* 2 × 1 mm; styles 4–5 mm long, 2–2·5 × ovary.



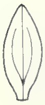
On steep north-facing sandstone slopes in subpáramo vegetation; 2360–2910 m.

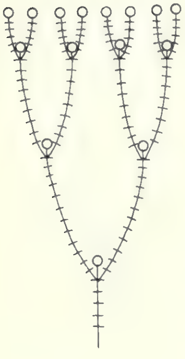
Venezuela (Sucre). Confined to the Cerro Turumiquire.
VENEZUELA. Sucre: Cerro de Turumiquire, 1925 (fl), *Tate* 329 (US).

52. **Hypericum ekmanii** A. H. Liogier

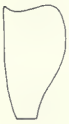
in *Phytologia* **47**: 183 (1980). Type: Dominican Republic, Peravia, San José de Ocoa, 2000 m, 4.vi.1978 (fl & fr), *A. & P. Liogier* 27672 (SDM, holotype; GH!, isotype).

Icon: Fig. 13B.





Shrub up to 0·75 m tall, erect, forming thickets, with branches ascending, pseudo-dichotomous and sometimes lateral. *Stems* orange-brown, 4-lined and compressed when young, the subfoliar ridges broad, soon 2-lined, eventually terete, cortex exfoliating at first in strips between subfoliar ridges; internodes 2–4 mm long. *Leaves* with short petiole (0·5–1 mm long), densely spreading or imbricate, tetrastichous, deciduous above petiole without fading; lamina 6–10 × 2–4 mm, elliptic, plane to slightly concave, scarcely cucullate, midrib not or slightly prominent beneath, margin incurved, not incrassate, concolorous, not glaucous or slightly so beneath, subcoriaceous; apex acuminate to apiculate, base angustate to cuneate, the petioles not sheathing but united to form very narrow interfoliar ridge; basal vein 1, with 1 short near-basal pair of branches or unbranched; laminar glands dense, visible on both sides. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 3–10 mm long, not incrassate upwards; upper leaves not transitional. *Flowers c.* 12–15 mm in diam., stellate. *Sepals* 5–6 × 1–2·5 mm, unequal to equal narrowly oblong to oblanceolate-spathulate, acute to subacuminate; veins 3, unbranched, with midrib not prominent, glands linear, punctiform in distal 1/4. *Petals* deep? yellow, 8–10 × 2–4 mm, *c.* 1·5 × sepals, oblong-oblanceolate; apiculus subacute; glands nearly all punctiform. *Stamens c.* 80, longest 5–6 mm long, *c.* 0·6 × petals. *Ovary* 2 × 1 mm, narrowly ovoid; styles 3, 5–6 mm long, 2·5–3 × ovary, diverging-incurved; stigmas clavate. *Capsule* 3–6 × 2–3 mm, ellipsoid, shorter than sepals. *Seeds* 1·2 mm long, ecarinate; testa finely ribbed-scalariform.



On rocky slopes in cloud forest; 1300–2550 m.

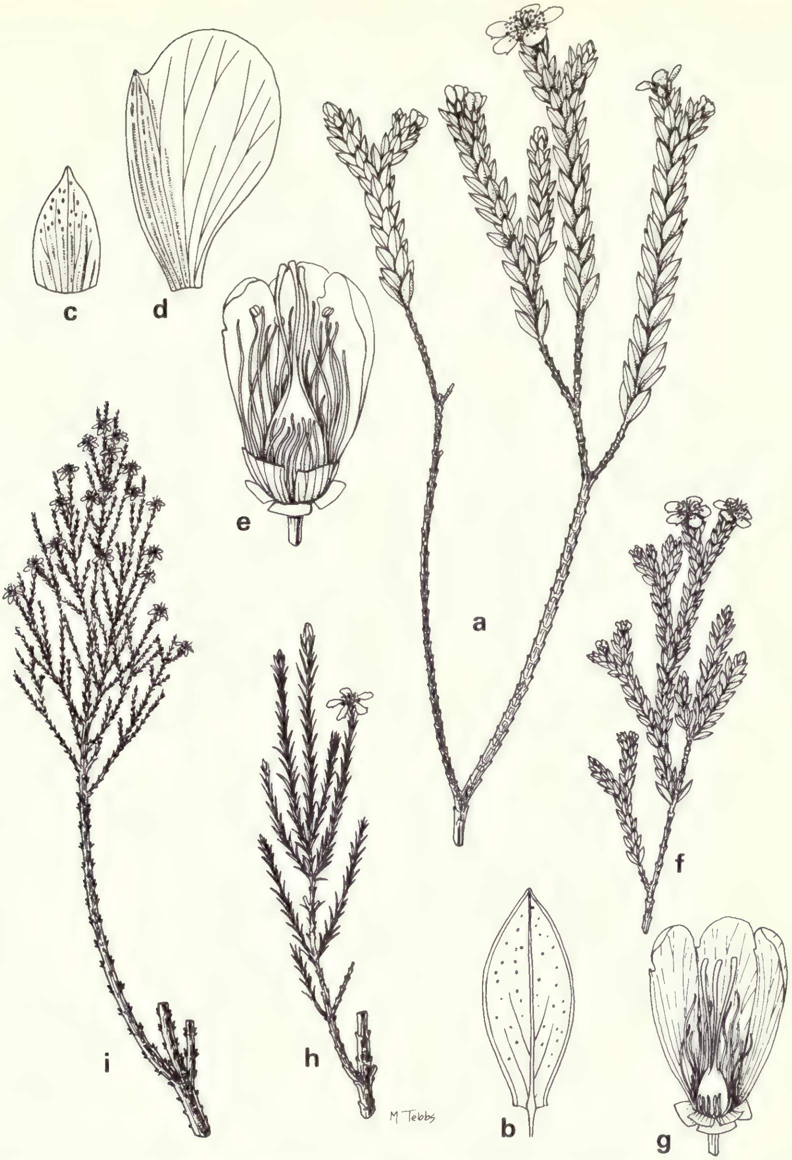
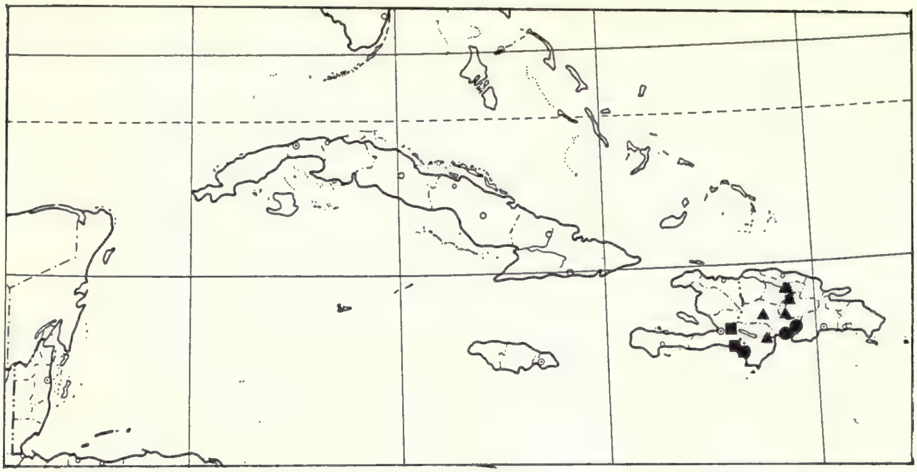


Fig. 13 A. *H. caracasanum* subsp. *caracasanum*: (a) habit; (b) leaf; (c) sepal; (d) petal; (e) stamens (partly cut away) and ovary. B. *H. ekmanii*: (f) habit; (g) stamens (partly cut away) and ovary. C. *H. pycnophyllum*: (h) habit. D. *H. millefolium*: (i) habit (a, f, h, i × ½; b × 2; c–e, g × 3). A. *Davidse & Gonzalez* 19550; B. *Ekman* 11718; C. *Liogier* 21790; D. *Holdridge* 1776.

Dominican Republic (Sierra de Ocoa). Map 21 (p. 92).

DOMINICAN REPUBLIC. Azua: Sierra de Ocoa, San José de Ocoa, S. slope of Tetero de Majía, *c.* 2550 m, 1.ii.1929 (fl & fr), *Ekman* H. 11718 (S, US).

Ekman (on the back of the label) states that the species is quite common in 'these mountains' (i.e. Sierra de Ocoa) and occurs at 1300 m near Bejucal. The gap in distribution between *H. ekmanii* (Hispaniola) and its nearest relative, *H. caracasanum* subsp. *turumiquirense* (NE. Venezuela), is likely to have resulted from long-distance dispersal and therefore cannot be adduced to support the theory that North and South America were originally linked via the Greater Antilles and the Yucatan Peninsula (see p. 9).

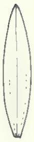


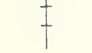
Map 21 52. *H. ekmanii* ● ; 53. *H. pycnophyllum* ▲ ; 54. *H. millefolium* ■.

53. **Hypericum pycnophyllum** Urban

Symb. Antill. **7**: 523 (1913). Type: Dominican Republic, La Vega, Loma Rosilla, 1700 m, 6.vii.1912 (fl), *Fuertes* 1749 (B†, holotype; NY!, P!, W!, isotypes).

Icon: Fig. 13C.





Shrub 0·2–1 m tall, erect, with branches very strict, pseudo-dichotomous and lateral. *Stems* reddish-brown, 2-lined and compressed when young, the subfoliar ridges broad, very soon terete, appearing articulated when old, cortex exfoliating at first in strips between subfoliar ridges; internodes 1–1·5 mm long. *Leaves* petiolate with short petiole (*c.* 0·5 mm long), densely imbricate, markedly tetrastichous, deciduous above petiole without fading or with attached cortex below after fading; lamina 3–9 × 0·5–2 mm, very narrowly elliptic to linear, incurved to canaliculate, ± cucullate, midrib impressed beneath, margin narrowly hyaline, dull above, lucent beneath, not glaucous, coriaceous; apex acute, base angustate to above 'articulation' then broadening, pairs forming narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense, obscure, visible above only. *Inflorescence* 1-flowered, terminal and on lateral branches, sometimes with single or pseudo-dichotomous branches from node below; pedicel absent or up to 3 mm long, not or slightly incrassate upwards; upper leaves not transitional. *Flowers* 10–20 mm in diam., stellate to obconic. *Sepals* 5–6(–7) × 1–2 mm, subequal, lanceolate to oblong-lanceolate, acute to acuminate, cucullate, with margin narrowly hyaline; veins 3–7, unbranched, midrib not prominent; glands linear, uninterrupted. *Petals* deep? yellow to orange-yellow, 7–14 × 3·5–7 mm, *c.* 1·6 × sepals, oblanceolate; apiculus acute; glands linear, distally interrupted. *Stamens* 55, longest 4·5–6·5 mm long, *c.* 0·6 × petals. *Ovary c.* 2 × 1 mm, ovoid; styles 3, 3·5–4 mm long, 1·5–2 × ovary, diverging-incurved; stigmas subclavate. *Capsule* 5–7 × 2·5–3 mm, narrowly ovoid, shorter than sepals. *Seeds c.* 1 mm long, ecarinate; testa finely ribbed-scalariform.

In open *Pinus occidentalis* forest and among rocks at higher altitudes; 1700–3175 m.

Dominican Republic (Santiago, La Vega, San Juan, Azua). Map 21.

DOMINICAN REPUBLIC. Azua: El Pico del Yaque, 3125 m, 3.i.1944 (st), *Jiménez* 232 (US). La Vega: Sabana Alte, *c.* 2700 m, 16.x.1929 (fl & fr), *Ekman* H. 13793 (S). San Juan: Pico Duarte, 3170 m, 10–14.vii.1976 (fl), *A. & P. Liogier* 25040 (NY). Santiago: Monción, top of Cerro Lucio, *c.* 2525 m, 12.vi.1929 (fl & fr), *Ekman* H.12850 (C, F, K, NY, S, US).

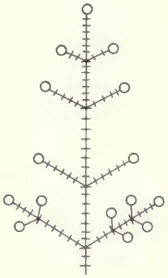
The specimens from higher altitudes have shorter leaves. *Hypericum pycnophyllum* is apparently more widespread than *H. ekmanii* and links it morphologically with *H. millefolium*.

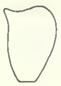
54. **Hypericum millefolium** Urban & Ekman

in *Ark. Bot.* **20** A, no. 15: 79 (1926). Type: Haiti, Massif de Selle, Morne de la Selle, Morne Emérillon, 2000 m, i.1925 (fl & fr), *Ekman* H. 3126 (B†, holotype; K!, NY!, S!, isotypes).

Icon: Fig. 13D.

Shrub up to *c.* 2 m tall, erect, juniperoid, with branches strict, pseudo-dichotomous (extension) and shorter, lateral (flowering). *Stems* 4–6-lined and ancipitous when young, persistently 4-angled and ancipitous until cortex exfoliates at first in strips between subfoliar ridges, then terete, fragile, green becoming pale grey; internodes 1–2 mm long. *Leaves* sessile, imbricate to curved-ascending, tetrastichous, eventually deciduous with attached cortex below after (?) fading; lamina 0·7–2 × 0·8–1 mm, lanceolate-triangular, incurved, markedly cucullate, midrib impressed beneath, margin narrowly hyaline, dull above, lucent or ± glaucous beneath, coriaceous; apex acute, pungent, base broad, subamplexicaul, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands obscure. *Inflorescence* 1-flowered, terminal and on numerous short lateral branches (branching or not), occasionally with pseudo-dichotomous branches from node below; pedicel absent or up to 0·5 mm long, incrassate upwards; upper leaves not transitional. *Flowers* 5–7 mm in diam., obconic. *Sepals* 3–3·5 × 1 mm, lanceolate, acute and incurved-cucullate to pungent; veins 5, unbranched, midrib ± prominent; glands linear, uninterrupted. *Petals* deep? yellow, 6–7 × 2·5–3 mm, 2 × sepals, oblanceolate; apiculus very acute; glands linear, distally subpunctiform. *Stamens c.* 50, longest 4–5 mm long, 0·6–0·7 × petals. *Ovary* 1·5 × 1 mm, broadly ovoid; styles 3, 4–5 mm long, *c.* 3 × ovary, diverging-incurved; stigmas narrow. *Capsule* 4 × 2 mm, ovoid, exceeding sepals. *Seeds* not seen.





Among steep limestone rocks; 1750–2350 m.

Haiti (Massif de la Selle). Map 21.

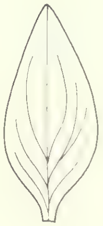
HAITI. Ouest: Massif de la Selle, Morne la Selle, Bouche Bouqui, 1750 m, 15.x.1943 (fl & fr), *Holdridge* 1776 (BM, MICH, NY, US); Croix des Bouquets, Morne Badeau, *c.* 2200 m, 24.ii.1927 (fl), *Ekman* H. 7679 (F, S, US), Pétionville, top of Morne Cabaio, 2350 m, 10.iv.1927 (fl), *Ekman* H. 7979 (C, S).

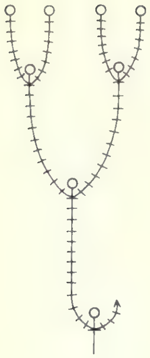
Hypericum millefolium, with its ericoid habit, is at first glance quite distinct from any other species in sect. *Brathys*. Closer investigation, however, shows it to be similar to the smaller form of *H. pycnophyllum*. Its triangular leaves and numerous fragile flowering stems, nevertheless, make it easily recognizable.

55. **Hypericum ruscoides** Cuatrec.

in *Ciencia Mex.* **4**: 63 (1943). Type: Colombia, Putumayo, Páramo de San Antonio del Bordoncillo, between El Encano and Sibundoy, 3250 m, 4.i.1941 (fl), *Cuatrecasas* 11720 (COL, holotype; F!, P!, US!, isotypes).

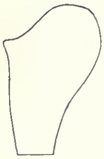
Shrub 0·1–1·5 m tall, erect or with stems sometimes decumbent and rooting at the base, with branches strict, pseudo-dichotomous and sometimes lateral. *Stems* yellow-brown, 4-lined and compressed when young, the subfoliar ridges broad, eventually terete, cortex exfoliating in strips between subfoliar ridges; internodes 2·5–6 mm long. *Leaves* petiolate with petiole 1·5–3·5 mm long, ascending to spreading, tetrastichous, deciduous above petiole without fading; lamina 8–18 × 3–6(–8) mm, narrowly ovate or lanceolate to narrowly oblong-elliptic or the uppermost elliptic, plane or slightly conduplicate, not or rarely carinate, slightly cucullate, midrib not or slightly impressed beneath, margin not distinct or rarely subincrassate, concolorous, sometimes ferrugineous, ± lucent or dull and undulate-papillose on both sides, sometimes glaucous, coriaceous; apex acute to apiculate, base angustate, the petioles not sheathing but united to form narrow interfoliar ridge; basal vein 1, with 2–4 pairs of obscure ascending branches, rarely visibly branched or reticulating; laminar glands dense, sometimes visible on either or both sides. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 4–8 mm





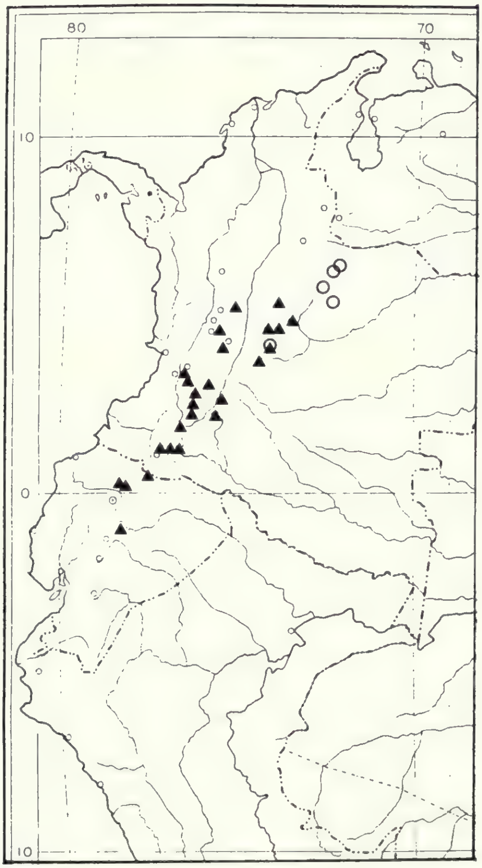
long; upper leaves often broader but not transitional. *Flowers* 15–25 mm in diam., stellate. *Sepals* 5–10 × 1–5–4 mm, obovate-spathulate to narrowly oblong (unequal to subequal), acute to obtuse; veins 5, branched or not, midrib not prominent; glands linear, distally punctiform. *Petals* deep yellow to orange-yellow, 8–15 × 4–6 mm, *c.* 1·5 × sepals, obovate-spathulate; apiculus subacute to obtuse; glands linear, distally punctiform. *Stamens* 30–60, longest 4–6·5 long, *c.* 0·5 × petals. *Ovary* 2–3 × 1·5–2 mm, ovoid; styles 3, 2·5–4 mm long, *c.* 1·3 × ovary, suberect to divergent; stigmas broadly capitate. *Capsule* 4–8 × 3–3·5 mm, cylindric-ellipsoid to ellipsoid, shorter than sepals. *Seeds c.* 1·5 mm long, ecarinate; testa finely scalariform.

In páramo; 2450–3800 m.



Colombia (Cordilleras Oriental, Central and Occidental from Boyacá and Cundinamarca to Putumayo), Ecuador (Pichincha and Napo: Volcán Cayambe). Map 22.

COLOMBIA. Boyacá: Villa de Leiva, Parque Igaque, Quebrada Carrizal, 3400 m, 25.xi.1984 (fl & fr), *Wood* 4621 (K). Caldas: Navarco, 3000 m, 12.ix.1951 (fl), *Romero-Castañeda* 3021 (COL). Cauca: Cordillera Central, Páramo de las Moras, 3800–3700 m, 19.ii.1969 (fl), *Cuatrecasas* 27424 (BM, COL, US). Cundinamarca: Municipio de Fomeque, páramo de Chingaza, cerros vecinos a la Laguna y limites con el Depto. del Meta, 3300 m, 2.xi.1966 (fl), *Huertas & Camargo* 6572 (COL). Huila: Cordillera Oriental, 20 km SE. of Gigante, 20.ix.1944, *Little* 8687 (COL). Meta: Páramo de Sumapaz, Cerro Nevado de Sumapaz, 3725 m, 29.i.1972 (fl), *Cleef* 1206 (BM, COL, U). Nariño: Pasto a Sibundoy, *c.* 3000 m, 5.i.1952 (fl), *Fernandez & Knoth* 1023 (COL). Putumayo: Valle de Sibundoy, Sibundoy, 2800 m, 30.vi.1953 (fl), *Schultes & Cabrera* 20138 (GH, NY). Tolima: Cordillera Central, Municipio de



Map 22 55. *H. ruscoides* ▲; 60, *H. selaginella* ○.

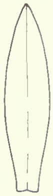
Roncevalles, páramo de Normandía, 3200 m, 8.xi.1980 (fl), *Camargo* 7508 (COL). Valle: Cordillera Occidental, Los Farallones, cerro Alto de Buey, 3500–3600 m, 11.x.1944, *Cuatrecasas* 17917 (BM, F, US), 17940 (COL).

ECUADOR. Pichincha: Cordillera Oriental, Laguna de Chiqui, NE. of Cayambe, 3800 m, 4.vi.1944 (fl), *Acosta Solís* 8151 (F). Napo: ENE. of Cayambe Mtn, 3210 m, 6.xii.1961, *Cazalet & Pennington* 5522 (K, NY).

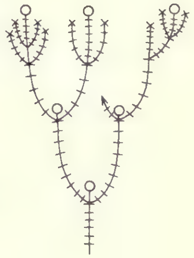
Hypericum ruscoides is related to *H. jaramilloi*, being intermediate between it and *H. lancioides*. It can easily be confused with reduced forms of *H. pimeleoides* in the area where the ranges of these species overlap, but can be recognized by the usually narrower and less crowded leaves with longer, narrower petioles, acute apex, and no free veins, i.e. the venation is pinnate.

H. ruscoides appears to be rare in the Cordillera Occidental. Two collections from Valle de Cauca, Los Fardallones, cerro Alto del Buey (*Cuatrecasas* 17917, 17940) have thinner, narrower, more shortly petiolate leaves than usual, and are nearest in form to *H. lancioides*. Cuatrecasas has distinguished them as 'var. *occidentale*' on the labels, and if these characters are constant in Cordillera Occidental populations, then this population may warrant recognition as a subspecies.

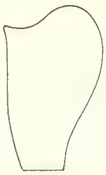
56. **Hypericum llanganaticum** N. Robson, **sp. nov.**



H. struthiolifolio Juss. affinis, sed statura alta, ramis haud radicantibus, foliis planis vel incurvatis, manifeste tetrastichis, plusminusve glaucis, sepalis oblongo-oblanceolatis haud porcatis, differt. Type: Ecuador, Napo, Llanganati, páramo SE. of Chosa Aucacocha, between Aucacocha and Pan de Azúcar, 3800–3900 m, 15.v.1982 (fl), *Øllgaard, Holm-Nielsen et al.* 38464 (AAU!, holotype).



Shrub 0·4–2 m tall, erect to decumbent but not rooting, with branches strict, pseudo-dichotomous or lateral. *Stems* orange-brown, 4-lined and ancipitous when young, eventually terete, cortex exfoliating in irregular flakes; internodes 1–2 mm long. *Leaves* sessile or rarely subsessile, erect to narrowly spreading, ± imbricate-tetrastichous, deciduous above the base after fading; lamina 7–13 × 1·5–4 mm, narrowly elliptic to linear-oblong, plane or slightly incurved, scarcely to markedly cucullate, midrib impressed beneath, margin not or very narrowly hyaline, concolorous, rather glaucous, ± coriaceous; apex acute, base angustate, not sheathing, pairs united to form rather shallow interfoliar ridge; basal vein 1, (always?) unbranched; laminar glands dense, visible above and rarely also beneath; marginal glands rather dense. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 3–4 mm long; upper leaves not transitional. *Flowers c.* 20–25 mm in diam., stellate. *Sepals* 7·5–9 × 1·8–2·3 mm, oblong-oblanceolate, acute, not or slightly incurved-cucullate; veins 5, branched, not or scarcely prominent beneath; glands striiform to punctiform. *Petals* (bright?) yellow, 12–16 × 4–10 mm, *c.* 1·5–1·8 × sepals, oblong-oblanceolate; apiculus acute; glands linear to striiform. *Stamens c.* 80–90, longest 6–10 mm long, 0·5–0·7 × petals. *Ovary c.* 3 × 2·5 mm, broadly ovoid; styles 3, 3·6–4·3 mm long, 1·2–1·4 × ovary, divergent; stigmas not or narrowly capitate. *Capsule c.* 5·5 × 3·5 mm, ovoid-pyramidal, shorter than sepals. *Seeds* not seen.

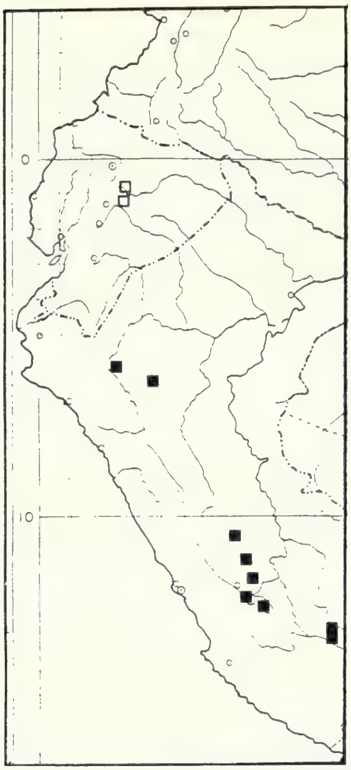


In grassy páramo with scrub or reed forest; 3250–4200 m.

Ecuador (Tungurahua, Napo). Confined to the Cordillera de Los Llanganates. Map 23 (p. 96).

ECUADOR. Napo: Cordillera de Los Llanganati, Chihuila o Ainchilibi, 3750 m, 25–29.viii.1959 (fl), *Barclay & Juajibioy* 8996 (MO, NY); junction of Río Chalupas and Río Agua Buenas, E. end of upper Chalupas valley, 3250 m, 11.viii.1979 (fl), *Holm-Nielsen* 19074 (AAU). Tungurahua: Cordillera de Llanganates, near Las Torres, 3700–3800 m, 22.xi.1939 (fl), *Asplund* 9878 (S); Llanganati Mts., Lake Aucacocha, 3700 m, vii.1969 (st), *Edwards* 35 (K).

H. llanganaticum comprises a relict population intermediate in form and distribution between *H. ruscoides* and *H. struthiolifolium*. *Asplund* 9878 differs from the other specimens in its broader leaves and thus approaches *H. ruscoides*, differing from it



Map 23 56. *H. llanganaticum* □; 57. *H. struthiolifolium* ■.

essentially only in the narrower leaves with a slightly cucullate apex and narrower stigmas. The remaining specimens are nearer to *H. struthiolifolium* but differ from it in having more crowded tetrastichous leaves (which are dull blue-green or glaucous, not lucent) and unribbed, oblanceolate to oblong sepals.

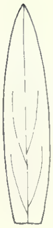
57. **Hypericum struthiolifolium** Juss.

in *Annls Mus. Hist. nat. Paris* **3**: 161, t. 16, f.2 (1804) ['*struthiolaefolium*']; Choisy, *Prodr. monogr. fam. Hypéric.*: 58 (1821), in DC., *Prodr. syst. nat. regni veg.* **1**: 553 (1824); R. Keller in *Bull. Herb. Boissier* II, **8**: 176 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925). Type: Peru, without precise locality or date (fl & fr), *Dombey* s.n. (P-JUS!, holotype; F!, P!, isotypes).

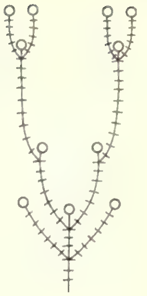
Brathys struthiolifolia (Juss.) Spach, *Hist. nat. vég.* Phan. **5**: 449 (1836) ['*struthiolaefolia*'], in *Annls Sci. nat.* II, **5**: 366 (1836).

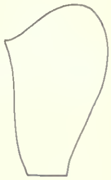
H. struthiolifolium var. *genuinum* Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 293 (1862) ['*struthiolaefolium*'], pro parte excl. spec. cit.

H. weberbaueri R. Keller in *Bot. Jahrb.* **42**: 129 (1908), in *Bull. Herb. Boissier,* II, **8**: 178 (1908), in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **21**: 181 (1925); Gleason in *Bull. Torrey bot. Club* **56**: 102, 103, 105 (1929), pro parte quoad typum. Type: Peru, Junin, Tarma, Huacapostana, 3000–3100 m, n.d. (fl & fr), *Weberbauer* 2093 (B†, holotype; F!, GH!, NY!, US!, photographs; G!, isotype).



Shrub up to *c.* 0·5 m tall, erect or sometimes decumbent and rooting, with branches strict, pseudo-dichotomous or sometimes lateral. *Stems* orange-brown, 4-lined and ancipitous when young, eventually terete, cortex exfoliating in irregular flakes; internodes 2–7 mm long. *Leaves* sessile, suberect to spreading or slightly outcurving, not or scarcely imbricate, deciduous above the base after fading; lamina 8–15 × 1·5–2·5 mm, very narrowly elliptic to linear-oblong, ± incurved- cucullate, midrib mostly impressed beneath, margin not or slightly hyaline, concolorous, lucent, not glaucous, ± coriaceous; apex acicular to subacute, base angulate, not sheathing, pairs united to form shallow interfoliar ridge; basal vein 1, occasionally with 1–2 pairs of obscure branches; laminar glands rather dense, visible above but not beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 5–9 mm long; upper leaves not transitional. *Flowers* 15–25 mm in diam., stellate. *Sepals* 5–8 × 1–3 mm, ovate-lanceolate to oblong, acute, incurved-cucullate; veins 5–9, not branched, prominent beneath; glands linear, punctiform in distal third. *Petals* bright yellow, (8–)10–15 × 3–7 mm, *c.* 1·5 × sepals, oblong-oblanceolate to oblong-obovate; apiculus acute; glands striiform. Stamens 60–75, longest 5–9 mm long, 0·5–0·6 × petals. *Ovary* 2·5–3·5 × 1·5–2 mm, broadly ovoid; styles 3(4), 3–4 mm long, 1·3–1·5 × ovary, spreading; stigmas not or narrowly capitate. *Capsule* 4–5 × 2–2·5 mm, ellipsoid, shorter than sepals. *Seeds c.* 0·7 mm long, ecarinate; testa finely scalariform.





On open hillsides among shrubs; 3000–3700 m.

North and Central Peru (Amazonas, Pasco, Junin, Huancavelica, Cuzco). Map 23.

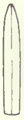
PERU. Amazonas: Chachapoyas, Pass of Piscohuañuna, 2700 m, viii.1938 (fl), *Sandeman* 239 (K); Bagua, Cordillera Colán E. of La Peca, 2880 m, 8.viii.1978 (fl), *Barbour* 3230 (MO). Cuzco: Urubamba, Puyupatamarca area, 3200 m, 29.iii.1894 (fl), *Vargas* 2762 (F). Huancavelica: Tayacaja, between Marcavalle and Huachocolpa, 3600 m, 24.iv.1963 (fl & fr), *Rovar* 4225 (NY). Junin: Chilifruta to Huancayo, 11 km, 3700 m, 30.x.1968 (fl), *B. & C. Maguire* 61657 (BM, NY). Pasco: Oxapampa, Cordillera Yanachaga 12 km SE. of Oxapampa, 2700–2800, 7.x.1982 (fl), *Foster* 9048 (BM, MO).

H. struthiolifolium was one of the first species in sect. *Brathys* to be described, and the name has frequently been misapplied. The species is confined to north and central Peru, where it is apparently relatively uncommon. It differs from *H. llanganaticum* in the less crowded, more incurved, lucent (not glaucous) leaves and the usually smaller flowers with sepals that are ribbed and usually broader below the middle. Also, its decumbent stems sometimes root. Its distribution overlaps considerably that of the derivative *H. andinum*, but these species remain distinct.

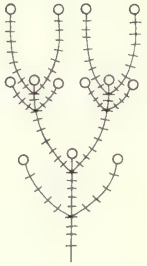
58. **Hypericum andinum** Gleason

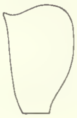
in *Torreya* **29**: 137 (1929). Type: Bolivia, Mt. Tunare, 1891 (fl & fr), *Bang* 1026 (NY!, holotype; BM!, F!, GH!, K!, MO!, US!, W!, isotypes).

H. struthiolifolium var. *parviflorum* R. Keller in *Bull. Herb. Boissier* II, **8**: 182 (1908) ['*struthiolaefolium*']. Type: Bolivia, La Paz, Larecaja, Majabaga, Catarguata, 2800–3200 m, x.1858–v.1859 (fl & fr), *Mandon* 790 (G!, holotype; BM!, GH!, K!, NY!, P!, S!, W!, isotypes).



Shrub or shrublet 0·1–0·5 m tall, erect or decumbent and rooting, bushy with branches strict, pseudo-dichotomous or lateral. *Stems* reddish to yellowish-brown, 4-angled when young, soon 2-lined then terete, cortex exfoliating in irregular flakes; internodes 1–4 mm long. *Leaves* sessile, suberect to outcurved, subimbricate to spreading, deciduous above the base after fading; lamina 3·5–10 × 0·8–1·5 mm, narrowly oblong-elliptic to linear, incurved-cucullate, midrib mostly impressed beneath, margin ± narrowly hyaline, otherwise concolorous, not glaucous, subcoriaceous to chartaceous; apex acute to rounded, base cuneate to parallel, not sheathing, pairs united to form shallow interfoliar ridge; basal vein 1, unbranched; laminar glands dense, impressed, visible beneath. *Inflorescence* 1-flowered, with pseudo-dichotomous branches from node below; pedicel 3–6 mm long; upper leaves not transitional. *Flowers* 10–18 mm in diam., stellate. *Sepals* 3·5–7 × 0·8–2 mm, broadly to narrowly lanceolate, subacuminate to acute, cucullate, with hyaline margin; veins (3)5(7), unbranched, ± prominent; glands linear, punctiform, in distal third. *Petals* golden yellow, 6–10 × 3–5 mm, *c.* 1·5 × sepals, narrow obovate to obovate-oblong; apiculus acute to obtuse or obsolete; glands shortly striiform to punctiform. *Stamens* 20–50, longest 3–6 mm long, *c.* 0·5 × petals. *Ovary* 1·8–2·3





(–3·3) × 1–1·2 mm, narrowly ovoid; styles 3, 1·5–2·5 mm long, 0·6–0·7 × ovary, free, spreading; stigmas broadly capitate. *Capsule* 4–6 × 1·2–3 mm, ovoid, shorter than sepals. *Seeds* not seen.

On open or stony grassy slopes and *Sphagnum* bogs, sometimes near the snowline; 2400–4200 m.

Peru (La Libertad, Junin, Huancavelica, Cuzco, Puño), Bolivia (La Paz, Cochabamba, Santa Cruz). Map 24.

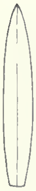
PERU. Cuzco: Paucartambo Valley, 26 km from Cuzco to Pilcopata, 3425 m, 27.ix.1968 (fl), *B. & C. Maguire* 61564 (BM, NY). Huancavelica: Tayacaja, between Colcabamba and Paucarbamba, Arriba de la Hda. Jocas, 3900 m, 20.iv.1954, *Tovar* 2020 (NY). Junin: Huancayo, ii.1939 (fl), *Soukup* 389 (F). La Libertad: Huamachuco, Jalca de Huaguil, 3950 m, 24.vi.1958 (fl), *López & Sagástegui* 2736 (NY). Puño: Ayapata, vi.1854 (fl & fr), *Lechler* 1817 (K, P, W).

BOLIVIA. Cochabamba: Road to Chapare [from Cochabamba], Km 104, 3100 m, 23.xii.1926, *Steinbach* 650 (F, MO, NY, S, U, US, WIS). La Paz: Sorata, 3900 m, ii.1886 (fl & fr), *Rusby* 1350 (MICH, NY). Santa Cruz: Comarapa, Cerro de San Mateo, 3400 m, 25.x.1928 (fl & fr), *Steinbach* 8535 (BM, F, GH, K, MO, NY, S, U).

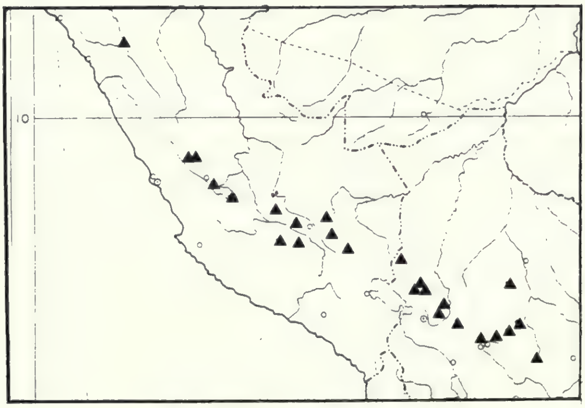
Although the area of *H. andinum* overlaps considerably that of *H. struthiolifolium*, the former can be distinguished by the shorter capitate styles and the narrower, usually less acute, recurving leaves with markedly hyaline margins.

59. **Hypericum lancioides** Cuatrec.

in *Ciencia Mex.* **4**: 65 (1943). Type: Colombia, Putumayo, Páramo de San Antonio del Bordoncillo, between El Encano and Sibundoy, 3250 m, 4.i.1941, *Cuatrecasas* 11721 (COL, holotype; F!, US!, isotypes).



Shrub c. 0·1–1 m tall, erect and bushy or ± decumbent and caespitose, branches strict, pseudo-dichotomous and lateral, or spreading (very rarely pinnate). *Stems* orange-brown, 6-lined and compressed when young, the subfoliar ridges broad, eventually terete, cortex splitting between and below subfoliar ridges; internodes 0·5–4(–6*) mm. *Leaves* sessile or rarely narrowing to a pseudopetiole up to 2 mm long, ascending to subimbricate, sometimes tetrastichous, deciduous above base (or pseudopetiole) after twisting spirally; lamina 7–15 × 1–1·4(–4*) mm, very narrowly elliptic-oblong to linear incurved to canaliculate or rarely subconduplicate, ± markedly cucullate, midrib impressed beneath, margin distinct, narrowly to rather broader hyaline, concolorous, lucent beneath, undulate-subpapillose above, glaucous or not, coriaceous to somewhat succulent; apex acute, base angustate to parallel-sided, not or scarcely sheathing, pairs united to form narrow interfoliar



Map 24 58. *H. andinum* ▲.

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* See note on p. 99.

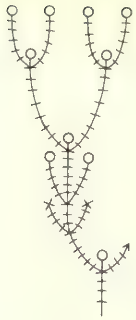
ridge; basal vein 1, unbranched; laminar glands rather sparse, usually visible above only but sometimes biseriate beneath. *Inflorescence* 1(3)-flowered, with pseudo-dichotomous branches from node below and sometimes short, often congested, lateral branches (racemiform); pedicel absent or up to 4 mm long; upper leaves not transitional. *Flowers* 10–16 mm in diam., stellate. *Sepals* (5–)6–8 × 0·5–1·5 mm, oblanceolate-oblong to oblong or rarely linear, unequal to subequal, acute, cucullate, margin ± broadly hyaline; veins 3–5, unbranched or outer branched, all not or slightly prominent; glands linear, punctiform in upper third. *Petals* yellow, 8–11 × 2·5–4 mm, *c.* 1·5 × sepals, narrowly obovate-oblong; apiculus acute to acuminate; glands linear, distally punctiform. *Stamens* 25–40, longest 3·5–5 mm long, *c.* 0·5 × petals. *Ovary* 1·5–2·5 × 0·8–1·5 mm, ellipsoid to subglobose; styles 3(4), 1–2(–3*) mm long, 0·5–0·9(–1·1*) × ovary, outcurved to suberect; stigmas broadly capitate. *Capsule* 4–5 × 1·5–2·5 mm, ovoid-ellipsoid to cylindric-ellipsoid, shorter than sepals. *Seeds* 0·8–1 mm long, ecarinate; testa finely scalariform.

In damp (sometimes marshy) or sheltered areas of the open páramo; 2870–4700 m.

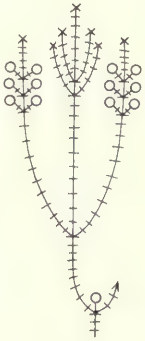
Western Venezuela (Mérida), Colombia (Santandér to Nariño) and northern Ecuador (Carchi to Cotopaxi). Map 25.

H. lancioides differs from *H. ruscoides* especially in its narrower, 1-veined, sessile leaves, narrower sepals and shorter styles. One collection from Colombia, Putumayo (*Schultes & Villareal* 7821), has relatively broad, petiolate leaves and longer styles (see characters marked*), and *Cuatrecasas* 17861 (Valle, Los Farallones, cerro La Torre) is even closer to *H. ruscoides* and could be of hybrid origin.

H. lancioides is variable and comprises two subspecies, one (subsp. *lancioides*) with its most primitive form in southern Colombia and extending from there north to Cundinamarca and south to Cotopaxi, has a simply pseudo-dichotomous inflorescence, whereas the other (subsp. *congestiflorum*) occurs from Cauca north-east to Mérida and has lateral flowers crowded below the terminal flower. Intermediate specimens between the subspecies occur in Cauca.



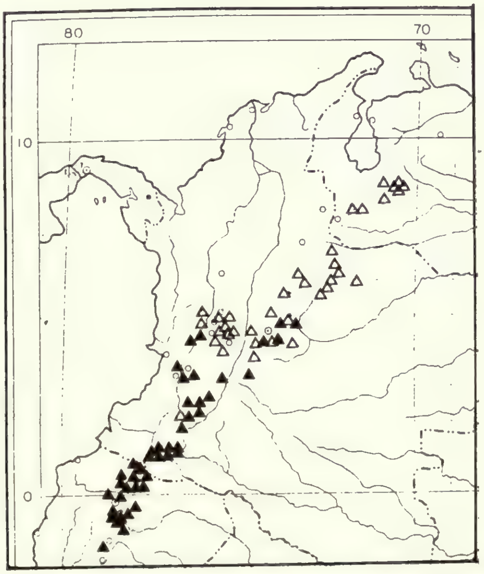
a



b

59a. **Hypericum lancioides** Cuatrec. subsp. **lancioides**

H. struthiolifolium var. *genuinum* Triana & Planchon in *Annls Sci. nat.* (Bot.) IV, **18**: 293 (1862) ['*struthiolaefolium*'] pro parte, quoad spec. cit.



Map 25 59. *H. lancioides* a. subsp. *lancioides* ▲, b. subsp. *congestiflorum* △.

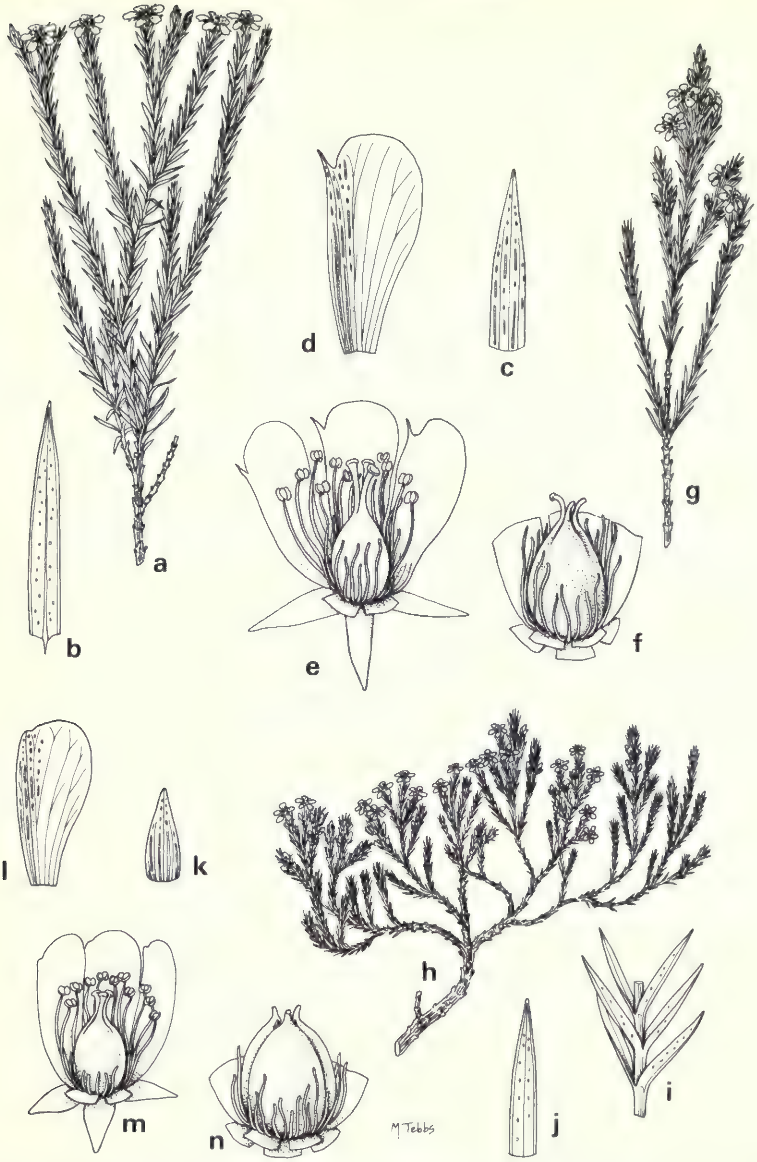


Fig. 14 A. *H. lancioides* subsp. *lancioides*: (a) habit; (b) leaf; (c) sepal; (d) petal; (e) stamens (partly cut away); (f) capsule. B. *H. lancioides* subsp. *congestiflorum*: (g) habit. C. *H. selaginella*: (h) habit; (i) stem with leaves; (j) leaf; (k) sepal; (b) petal; (m) stamens (partly cut away) and ovary; (n) capsule (a, g, h × ½; b–f × 3; i–m × 4). A. *B. & C. Maguire* 61808; B. *Cuatrecasas et al.* 28120; C. *Barclay & Juajibioy* 7407.

H. strictum sensu Gleason in *Bull. Torrey bot. Club* **56**: 102 (1929) pro parte, quoad spec. cit.

H. lancioides forma *pygmaea* Cuatrec. in sched.

Icon: Fig. 14A.

Shrub 0·2–1 m tall, erect, bushy, with branches strict, pseudo-dichotomous and lateral. *Leaves* shortly petiolate or sessile, usually spreading, sometimes ± tetrastichous, very narrowly elliptic or oblanceolate to linear. *Inflorescence* branches pseudo-dichotomous with flowers solitary, terminal and sometimes on well-developed branches from lower nodes. *Sepals* oblong to linear, with veins prominent.

3000–4100 m.

Southern Colombia (Cundinamarca and Meta southwards) and Ecuador (Carchi to Cotopaxi).

COLOMBIA. Cauca: Cordillera Central, Páramo de las Moras, 3800–3700 m, 12.xii.1969 (fl & fr), *Cuatrecasas* 27419 (BM, COL, US). Cundinamarca: Cordillera Oriental S. of Usmé, páramo de Chisaca above Laguna Grande and L. Negra, 9–11.xi.1958 (fl), *Barclay & Juajibioy* 6191 (COL, MO, NY). Huila: Municipio de La Plata, Inspección de Policía de Santa Leticia, Páramo de La Candelaria, 2370 m, 15.vii.1975 (fl), *Díaz, Lozano & Torres* 595 (COL). Nariño: Province de Pasto, Fuguerres, 300 m, v.1853 (fl), *Triana* 5464 (BM, COL, K, MEXU, NY, P, W); Volcán El Galeras, *c.* 3200–3500 m, 4.vi.1946, *Schultes & Villareal* 7960 (COL, F). Putumayo: Pasto to Sibundoy, Páramo de San Antonio, 2790–2880 m, 13.iii.1953 (fl & fr), *Schultes & Cabrera* 18828 (COL, GH, NY, U). Valle: Cordillera Occidental, Los Farrallones, cerro de La Torre, La Laguna, 3500–3550 m, 1.viii.1946 (fl), *Cuatrecasas* 21870 (BM, F, P, U, US).

ECUADOR. Carchi: Tulcán to Maldonado, *c.* 43 km, SW. slopes of Volcán Chilas, 3740 m, 6.viii.1976 (fl), *Øllgaard & Balslev* 8549 (AAU, BM). Cotopaxi: Ruminahui, 3850 m, 17.ii.1947 (fl & fr), *Aubert de La Rue* s.n. (P). Imbabura: Lago San Marcos, Cayambe, 3360 m, 26.xi.1961 (fl), *Cazalet & Pennington* 5349 (K). Napos: Laguna Porjuantag, ENE. of Volcán Cayambe, 3750 m, 10.ii.1953 (fl), *Prescott* 347 (NY). Pichincha: Paso de Guamani, 35–37 km ESE. of Quito, headwater of Río Papallacta, 23.v.1947 (fl), *Fosberg* 27609 (NY, US); Cordillera Oriental, environs of Laguna de Chiquí, 3800 m, 4.vi.1944 (fl & fr), *Acosta Solís* 8176 (F).

59b. **Hypericum lancioides** Cuatrec. subsp. **congestiflorum** (Triana & Planchon) N. Robson, **comb. et stat. nov.**

H. struthiolifolium var. *congestiflorum* Triana & Planchon [ex Weddell, *Chloris Andina* **2**: 271 (1857) '*struthiolaefolium*', nomen] in *Annls Sci. nat.* (Bot.) IV, **18**: 294 (1862) pro parte, excl. syn.; Knuth in *Reprium Spec. nov. Regni veg.* Beih. **43**: 484 (1927) pro parte, excl. spec. *Funck & Schlim* 1140. Type: Venezuela, Mérida, Sierra Nevada de Mérida, 2870 m, 1842 (fl), *Linden* 432 (COL?, holotype; P!, isotype).

Icon: Fig. 14B.

Shrub 0·1–0·5 m tall, erect and bushy or decumbent and caespitose with branches strict, lateral (very rarely pinnate), spreading. *Leaves* sessile, ascending to imbricate, tetrastichous, linear. *Inflorescence* branches elongate, sympodial (from terminal node) and very short, lateral, with flowers solitary or in triads in a congested spiciform thyrse, immediately below terminal flower or with several intervening sterile nodes. *Sepals* oblong-lanceolate, with veins not or slightly prominent.

2870–4500 m.

Western Venezuela (Mérida), north-eastern and central Colombia (Santandér to Cauca).

COLOMBIA. Arauca: Sierra Nevada del Cocuy, Quebrada El Playón, Plan de S. José, 3625 m, 9.vi.1973 (fl), *Cleef* 10051 (U). Boyacá: Páramo de Chitá, cabeceras del Río Casanare, Hoya Laguna Chorros Blancos, 3340 m, 24.v.1973 (fl), *Cleef* 9931A (COL, U). Caldas: Páramo del Quindio, 4100–4300 m, 15–20.viii.1922 (fl), *Pennell & Hazen* 9874 (GH, K, S). Cauca: Páramo de Purace, 3500 m, 26.v.1944 (fl), *Killip & Lehmann* 38548 (COL). Cundinamarca: Páramo de Palacio, *c.* 600 m al NW. de Mina de Cal, 3520 m, 13.v.1972 (fl), *Cleef* 3733 (BM, COL, U); Lagunas de Buitrago, 3555 m, 27.iv.1973, *Cleef* 9588A (COL). Meta: Páramo de Sumapaz, Cerro Nevado de Sumapaz, 3615 m, 29.i.1972, *Cleef* 1269 (COL, U). Risaralda: Municipio de Pereira, alredores de la Laguna Otún, 4000–4300 m, 3.ii.1980 (fl), *Díaz, Valencia & Jaromillo* 1754 (COL). Santandér: Páramo del Almorzadero, 3500–3700 m, 20 vii.1940 (fl), *Cuatrecasas & Garcia Barriga* 9998 (COL, F). Tolima: Páramo de Herves, Eresno, 3600 m, 14.vii.1939 (fl), *Hanbury-Tracy* 603 (K).

VENEZUELA. Mérida: Páramo de Timotes, 3200 m, 25.i.1939 (fl), *Alston* 6616 (BM, NY); Quebrada de Saisay, 3880 m, 10.iv.1930, *Gehringer* 57 (NY, VEN).

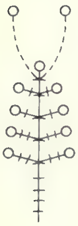
In Venezuela there is a tendency in subsp. *congestiflorum* towards regular pyramidal branching, shorter glandular-punctate leaves, and smaller flowers, sometimes with 4 styles. All these characters foreshadow *H. selaginella*.

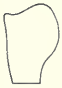
60. **Hypericum selaginella** N. Robson, **sp. nov.**

H. lancioidei subsp. *congestiflorae* (Triana & Planchon) N. Robson affinis, sed habitu nano prostratoque, ramificatione pinnato, foliis brevioribus dense imbricatis, flores minoribus, stylis (3)4–5 brevioribus, differt. Type: Colombia, Boyacá, Cordillera Oriental, Sierra Nevada del Cocuy, Alto Ritacuva, Station 16, *c.* 4400 m, 11–29.iv.1959 (fl & fr), *Barclay & Juajibioy* 7407 (COL!, holotype; MO!, NY!, isotypes).

H. selaginoides N. Robson in Cleef, *Veg. Páram. Colomb. Cord. Or.*: 305 (1981), nomen.

Icon: Fig. 14C.





Shrublet up to 0·15 m tall, prostrate or ascending, forming tufts up to 150 mm in diam., with branches pinnate, spreading. *Stems* orange-brown, 6-lined and compressed when young, the subfoliar ridges broad, eventually terete, cortex splitting between and below subfoliar ridges; internodes *c.* 0·5 mm long. *Leaves* sessile, densely to loosely imbricate, tetrastichous, deciduous above base or more usually only with the cortex after fading; lamina 4–7 × 0·5–0·8 mm, linear, incurved-canaliculate, cucullate, midrib impressed beneath, margin broadly hyaline, concolorous, sublucent beneath, sublucent to dull above, sometimes subglaucous, coriaceous; apex acute to subacute, base parallel-sided, not sheathing, pairs united to form narrow interfoliar ridge; basal vein 1, unbranched; laminar glands dense above, rather sparse or absent beneath. *Inflorescence* 1-flowered, with pseudodichotomous branches from node below and also short congested lateral branches (racemiform); pedicel absent or up to 2 mm long; upper leaves not transitional. *Flowers c.* 8 mm in diam., stellate. *Sepals* 3–4 × 0·8–1·2 mm, oblong to triangular-lanceolate (equal), acute, cucullate, margin broadly hyaline; veins 3(5?), unbranched, slightly prominent; glands mostly linear. *Petals* bright yellow, tinged red outside, 4·5–6 × 2–2·5 mm, 1·5 × sepals, obovate-oblong; apiculus very short or almost absent; glands linear, distally punctiform. *Stamens c.* 13, longest 3–4 mm long, *c.* 0·65 × petals. *Ovary* 1·5–2·5 × 1·5–2 mm, subglobose; styles (3)4–5, 0·8–1 mm long, 0·4–0·5 × ovary, outcurved; stigmas broadly capitate. *Capsule c.* 3 × 3 mm, cylindric-globose to globose, shorter than sepals. *Seeds* 0·7–0·8 mm long, ecarinate; testa finely scalariform.

In dry and stony or dampish páramo or superpáramo; 3300–4340 m.

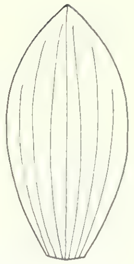
Colombia (Boyacá, Arauca, Cundinamarca), in the Sierra Nevada del Cocuy, Páramo de Pisva and Macizo de Sumapaz. Map 22 (p. 94).

COLOMBIA. Arauca: Sierra Nevada del Cocuy, Cabeceras de la Quebrada, El Playón, Patio Bolos, 2·5 km S. of Alto La Plaza, 4340 m, 9.iii.1973 (fl & fr), *Cleef* 8944 A (COL). Boyacá: Sierra Nevada del Cocuy, Valle de los Corallitos, *c.* 4300 m, 31.vii.1957 (fl), *Grubb, Curry & Fernandez-Perez* 178 (COL, K, US); Páramo de Pisva, Socha to La Punta Km 61.5, 6 km al NE. de Los Pinos, 3600 m, 10.vi.1972 (fl & fr), *Cleef* 4328 (BM, COL, U). Cundinamarca: Macizo de Sumapaz, Cuchilla La Rabona, 3900–3950 m, 17.vii.1981 (fl), *Díaz et al.* 2871 (COL).

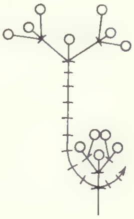
In *H. selaginella* the reduction trends of *H. lancioides* are continued. The different characters between it and *H. lancioides* subsp. *congestiflorum* (dwarf prostrate habit, smaller and more densely imbricate leaves, smaller flowers, shorter and usually more numerous styles) are clear-cut except for a few collections of the latter taxon from Mérida, which are somewhat intermediate in habit and size of parts.

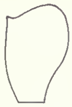
61. **Hypericum cymobrathys** N. Robson, **sp. nov.**

H. terrae-firmae Sprague & Riley affinis, sed habitu humiliori, foliis brevioribus crassioribus, interdum leviter cucullatis, supra basin deciduis, floribus minoribus in cymes 3–12-floris dispositis, 3-stylis, inter alia differt. Type: Colombia, Boyacá, La Uvita, by road from Chitá, 3000–3050 m, 16.ix.1969 (fl), *Cuatrecasas & Rodriguez* 27805 (COL!, holotype; BM!, US!, isotypes).



Shrub 0·5–1 m tall, erect, with branches ± strict, pseudo-dichotomous or occasionally lateral. *Stems* orange-brown to purplish-brown, 4-lined and markedly ancipitous when young, soon 4-angled, cortex exfoliating in irregular flakes; internodes 2–5 mm long. *Leaves* sessile, spreading from above base, tetrastichous, deciduous from above base without fading; lamina 9–18 × 3–8 mm, oblong to elliptic, plane, slightly cucullate, midrib prominent towards the base beneath, concolorous, glaucous, coriaceous; apex acute to obtuse, base cuneate to angustate, sheathing, saccate, pairs united to form narrow interfoliar ridge; basal veins 5–7, subparallel, apparently unbranched, tertiary reticulum not visible; laminar glands dense, prominent to ± impressed. *Inflorescence* 3–12-flowered, crowded (monochasial)?, with pseudo-dichotomous branches from node below; peduncle and pedicels 3–5 mm long, sometimes incrassate upwards; upper leaves intermediate, bracts narrowly elliptic-oblong, acute. *Flowers c.* 15 mm in diam., stellate or cyathiform. *Sepals* 6–8 × 2·2–2·4 mm, narrowly lanceolate, acute; veins 5(7), unbranched, with midrib slightly prominent; glands linear, distally striiform. *Petals* bright yellow, 8–9 × 3·5 mm, *c.* 1·2 × sepals, narrowly obovate; apiculus acute; glands linear, interrupted distally. *Stamens c.* 100, longest 4–5 mm long, *c.* 0·5 × petals. *Ovary* 2 × 1·5 mm, broadly ellipsoid; styles 3, 3 mm long, 1·5 × ovary, outcurving; stigmas narrow. *Capsule c.* 5 × 3 mm, broadly ellipsoid, shorter than sepals. *Seeds* 1·2–1·3 mm long, carinate; testa finely scalariform.





Shrubby woodland on dry slopes; 2970–3500 (–3900?) m.

Colombia (Boyacá). Apparently confined to a small area of the Cordillera Oriental around Guantiva and Chitá. Map 11 (p. 54).

COLOMBIA. Boyacá: Socha to Los Pinos, Km 41, 2970 m, 22.v.1973 (fl), *Cleef* 9871 (BM, U); Páramo de Guantiva, 3000–3900 m, 23.vii.1952 (fl), *Schneider* 1225 (S); Municipio de Tota, Cerro los Arcos, alredores de Lago de Tota, 3050 m, i.1976 (fr), *Aguirre & Rangel* 391 (COL).

Although the cymose inflorescence of *H. cymobrathys* is reminiscent of *H. mexicanum*, its flowers and leaves are very different. Its relationships appear to be with *H. terrae-firmae*, although the much smaller flowers, 3–12-flowered inflorescence, and smaller leaves make it superficially unlike it. Indeed, it appears to be an isolated relict species at the base of a clade that includes *H. chamaemyrtus, H. gnidioides*, and the *H. gentianoides* group, as well as *H. denticulatum* and its relatives (see part 8).

3. **Acknowledgements**

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5. Systematic index

Accepted names are in roman and synonyms in *italic*; new names are in **bold**, as are principal references. An asterisk (*) denotes a figure.

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Studies in the genus *Hypericum* L. (Guttiferae)

N. K. B. Robson

When completed in nine parts, this series of papers will constitute a monograph of *Hypericum*, St John's wort. This ancient genus, with an almost world-wide distribution, is of great scientific interest, as well as of considerable importance in horticulture and, to a lesser extent, pharmacy. Parts 1 (1977) and 2 (1981) are introductory, and the detailed taxonomy begins with part 3 (1985), in which the first seven sections (sects 1–6a) are treated. The present paper (part 7) contains the majority of sect. 29, the remainder of which will be included in part 8, along with accounts of sects 30 and 31. Subsequent papers (parts 4–6) will contain treatments of sects 7–28, and the concluding paper (part 9) will contain addenda, corrigenda, a revised sectional key and enumeration, and a continuous numerical series of species.

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The lichen genus *Ramalina* in Australia

G. Nell Stevens

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The lichen genus *Ramalina* in Australia

G. Nell Stevens
Department of Botany, University of Queensland, St Lucia, 4067, Australia

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Synopsis

This paper presents a revision of the lichen genus *Ramalina* in Australia. Of the 60 *Ramalina* taxa previously listed for Australia in catalogues only nine of those names are retained, six with unchanged status. Twenty-eight taxa belonging to 20 species are recognized for Australia. Two are new species: *R. filicaulis* and *R. tropica*. A new variety *R. subfraxinea* var. *norstictica* and a new subspecies *R. inflata* subsp. *australis* are described, and four names, *R. celastri* subsp. *ovalis*, *R. inflata* subsp. *perpusilla*, *R. subfraxinea* var. *confirmata*, and *R. subfraxinea* var. *leiodea* are new combinations.

The taxonomically important features of this genus (viz. morphology, anatomy, and chemistry) are discussed. In delimiting taxa, the morphological plasticity shown by this genus has been taken into consideration so that a wide range in infraspecific variation has been accepted for some of the taxa. The distribution patterns of the Australian Ramalinae are shown to closely follow the distribution of Australian phanerogam groups, which are controlled by the environmental parameters of rainfall and temperature; this enables the Ramalinae to be conveniently divided into three response groups (viz. megatherm, mesotherm, and microtherm) as used to divide the Australian phanerogams. On the basis of species diversity it is hypothesised that the genus had its origin in west Gondwanaland (South America and Africa) and then spread to the east. It is suggested that subsequent speciation occurred within Australia.

Introduction

The genus *Ramalina* has been studied in the northern hemisphere for over two hundred years and several hundred taxa have been named. In the southern hemisphere very little research has been undertaken and no revisional work had been carried out on the Australian Ramalinae before the present study. During the course of previous research into the taxonomy and ecology of twenty-four lichen genera found on eastern Australian mangroves (Stevens, 1978) it became apparent how necessary it was for a revision of the Australian representatives of the genus to be undertaken.

This present work provides a taxonomic revision of the Australian Ramalinae as well as an ecological survey and a biogeographic assessment of the genus. Research into the Australian taxa in this genus also contributes to the overall understanding of the biogeography of allied *Ramalina* species which occur in the other Gondwanaland regions of Africa, India, and South America.

The genus is regarded as a difficult one and its morphological plasticity is renowned. Howe (1913–14) aptly summed up the dilemma when he stated 'there is little difficulty in recognizing the characteristics of the genus *Ramalina*. The species on the other hand, have presented a most difficult problem, caused largely no doubt by the innumerable intergrades that present themselves, and by the unwarranted description of new species'.

This problem was encountered by the author when confronted by the record of 60 different *Ramalina* taxa reported for Australia (Wetmore, 1963; Weber & Wetmore, 1972) in catalogues which listed all taxa recorded for Australia in papers published from 1804 to 1972. It was apparent quite early in the study that many of these names were incorrect; some were synonyms, others misapplication of the names of northern hemisphere species which they superficially resembled.

Other recent mention of Australian Ramalinae occurs in an unpublished key to the genus *Ramalina* by Dahl (1971) and in Filson & Rogers (1979), but in both of these accounts little preliminary research had been carried out before naming the taxa. Most of the existing literature summarizing Australian material was therefore of little help in the present study.

There are few modern publications recording research which include the southern hemisphere Ramalinae. Krog & Swinscow (1974, 1975, 1976) have published detailed work on the East African Ramalinae. Rundel (1978*a*) has dealt with the *Ramalina usnea* complex in North and South America and in a paper on the lichens of Tristan da Cunha, Jørgensen (1977) discussed six species of *Ramalina*. No other publications discuss this genus in detail; however, a series of papers by Osorio published from 1967 to 1983 list the lichens found in Uruguay, Paraguay, Brazil, and Argentina and these include some species of *Ramalina*. An account of the lichens of New Zealand (Galloway, 1985) which includes the genus *Ramalina* lists only nine species.

During the present research four months were spent in Europe and U.S.A. visiting herbaria (BM, FH, H, HAW, O, S, UPS and US) and becoming familiar with northern hemisphere *Ramalina* species. This enabled an insight to be gained into the reason why Australian species were often given the names of the northern hemisphere species. The type material of species which occur in other southern continents was also examined where possible.

In this study the approach has been to reinforce the taxonomic revision of the genus by incorporating ecological data in order to explain phenotypic variation, and to enable the delimitation of the taxa to be made more confidently. The extreme morphological variation within the species was a major problem. The extent of such variation in Australian material had not previously been gauged, nor was there any conception of the evolutionary relationships that might exist between the different taxa.

Many thousands of specimens therefore needed to be examined before any decisions could be made on the delimitation of species. Examination of too few specimens makes it impossible to understand the breadth of morphological plasticity exhibited by a single species, and the early taxonomy of Australian Ramalinae was based on single or at most several thalli which were usually collected by someone other than the taxonomist.

Collection of *Ramalina* material by the author began in 1975, when the lichens on mangroves were studied (Stevens, 1978). Since then collecting trips have covered parts of New South Wales, Victoria, Tasmania, Western Australia, and Northern Territory and innumerable collecting forays were made in many areas of Queensland. After several expeditions inland it was found that the genus *Ramalina* was restricted to a zone varying within 100–200 km of the coastline, thus eliminating the need to collect in the arid interior (Fig. 1).

Observation of the different ecological habitats occupied by any one species was made to enable an appreciation of the variation that occurs in the morphology of a species under different environmental pressures. As well as sampling different habitats in the one region, thalli were

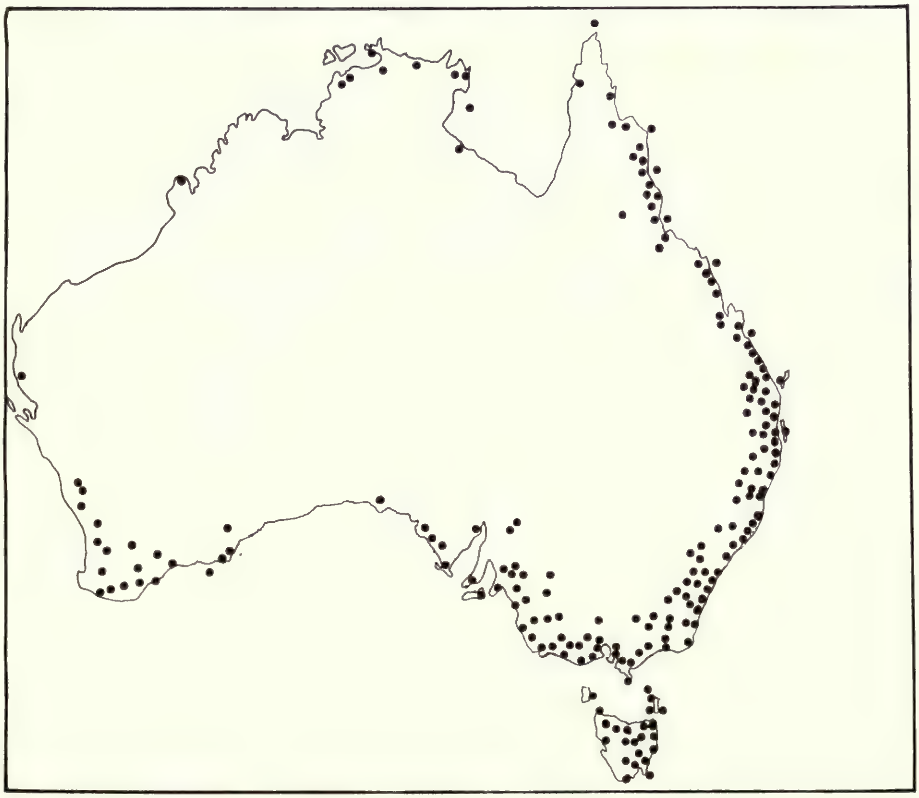

Fig. 1 *Ramalina* distribution in Australia.

collected (wherever possible) from latitude to latitude in order to assess if a continuum existed between the different morphologies found over a wide geographical range.

To a large extent this research has been carried out on personal collections of fresh material, supplemented by collections made by present day Australian lichenologists, material available from herbaria in each of the Australian states, and to a far lesser extent on old collections held in overseas herbaria. The latter proved to be of little use as only vague information concerning the location of the collection was ever recorded, e.g. New Holland. In contrast the Australian material was well documented on the whole but the specimens remained unnamed or bore doubtful identifications.

All of the Australian types were examined and, where possible, compared with fresh material from the type location. In this way the amount of variation that occurred within the particular species could be assessed. It was found in some instances that the type represented one extreme in a large population of morphotypes.

An attempt has been made to show possible evolutionary relationships between some of the taxa, based on morphological and/or chemical evidence associated with geographical patterns of distribution, as suggested by Imshaug & Brodo (1966).

This revision has treated all Australian material as belonging to the genus *Ramalina* Ach., as observations during the present study did not substantiate separation into the two genera *Ramalina* Ach. and *Fistulariella* Bowler & Rundel. No species belonging to any other divisions within the Ramalinaceae (Bowler, 1981) occur in Australia. A representative collection has been deposited in BM.

The Australian environment

Although it is beyond the scope of this study to provide a detailed discussion of the geography, climate, botany, and geology of Australia, a general outline is presented to enable a better appreciation of the factors which are influencing *Ramalina* distribution (Fig. 1).

(1) *Geography*

The area of Australia is approximately 8,700,000 km^2, larger than all of western Europe, and its immense coastline measures some 36,700 km. In total it comprises the Australian mainland, the large island of Tasmania, and numerous small islands around its coastline. It is washed by three oceans, the Pacific, Southern, and Indian, and four seas, the Tasman, Timor, Coral, and Arafura. It extends from approximately 9°30′S (Dauan Island in Torres Strait) to 43°S (southern Tasmania) and includes Macquarie Island at 55°S; its climate varies from equatorial through subtropical in the north to warm temperate, cool temperate to sub-antarctic in the south.

Overall the landmass is low: exceeding 1000 m in only very limited areas, most of these being close to the eastern coastline, predominantly in a north-south alignment through Queensland, New South Wales, and Victoria. This continuation of the Eastern Highlands and Great Dividing Range from north to south creates a fairly uniform topography which is conducive to species dispersal over a wide geographical area without creating any substantial barrier to the distribution, which could lead to endemism.

In the south this mountain range turns west through the Victorian Alps to the Grampians of western Victoria. Farther south the highland chain is apparent as islands in Bass Strait and in Tasmania. During times of low sea-level in the Pleistocene glacial period, these islands and Tasmania were joined to the mainland. Two endemic species have evolved, probably as a result of isolation of these islands from the continent. Several well separated parts of the mountain chain have individual mountains which exceed 1500 m elevation. These are found in Tasmania, the Victorian Alps, the Snowy Mountains, the New England Tableland in New South Wales, and Bellenden Ker Range in Queensland.

The majority of the western and southern Australian land mass is a vast flat peneplain with an elevation between 200 m and 500 m. In the north-west area the highest peak in the Hamersley Ranges exceeds 1200 m in height, and in central Australia the Macdonnell and Musgrave Ranges reach a similar height. Much of the interior of Australia is arid sand-ridge desert; the arid zone extends to the western and southern coasts between the moist south-west corner of Western Australia and the more fertile south-east of Australia. Extensive salt lakes occur in the south and south-western regions of the arid interior.

(2) *Climate*

The general climatic characteristics of Australia are dictated by its latitudinal position lying astride the mid-latitude high pressure belt. The prevailing wind patterns and general aridity over continental Australia reflect the dominating control of eastward-moving anticyclonic cells which track between 37°–38°S in summer and between 29°–32°S in winter. Seasonal change is linked with these sun-controlled shifts in the paths of the anticyclonic cells and associated movements of the south-easterlies and the inter-tropical convergence zone which influence the climate of eastern and northern Australia, and the westerlies which influence the climate of southern Australia and Tasmania (Nix, 1981).

Summer rainfall predominates in the north, winter rainfall in the south, and along the eastern coast a more uniform distribution of rainfall is common (Figs 2A & B). The eastern coastline of Australia receives a substantial rainfall, which ranges from over 2000 mm in north Queensland to 741 mm in Westernport Bay, Victoria. The western coastline receives far less precipitation per annum, partly due to the lack of any mountain ranges close to the coast. The annual precipitation ranges between 230 mm and 840 mm per annum with the highest recordings in the southwest corner where winter rains occur. Winter rainfall is predominant as far north as 24°S, then summer rainfall becomes dominant in the monsoonal area.

More than 80% of the continent has at least three months each year which are without effective precipitation (Nix, 1981). Two-thirds of Australia has less than 500 mm rainfall per annum and one-third less than 250 mm. Most of the coastline represents a moist rim around an otherwise dry continent; however parts of this coastline in South and Western Australia are also extremely arid, and no Ramalinae occur there. The absence of Ramalinae in the arid inland is possibly due to a combination of inhibiting factors such as high summer temperatures, low rainfall, and lack of a suitable substrate.

In tropical Australia the highest relative humidity occurs during the rainy summer season while in the temperate region relative humidity is generally highest in winter and lowest during the summer. The relative humidity variation during the day closely follows the diurnal variation of temperature, being highest with low temperatures and lowest with high temperatures.

Mean minimum temperatures occur in July throughout Australia. Freezing temperatures and frosts occur regularly below the 5°C isotherm and the frost-free limit coincides approximately with the 10°C isotherm. The ameliorating influence of the surrounding oceans is evident in the coastal areas of southern Australia and Tasmania. Rainfall is the dominant mode of precipitation, with sleet and snow confined to the higher mountains of southeastern Australia on the mainland and in Tasmania.

The greater part of the Australian land mass receives over 3000 hours of sunshine per year while the east coast is reported to receive between 2500 and 3000 hours, indicating that cloudiness is higher near the coast.

The Queensland coast as far south as Mackay and the Western Australian coast as far south as Carnarvon are subject to tropical cyclones, normally between December and March, which cause very heavy rainfall and accompanying strong winds. Sea surface temperatures around Australia range from 15°–30°C in summer to 12°–26°C in winter.

(3) *Botany*

Specht (1970) arbitrarily divided the Australian vegetation into structural formations based on foliage cover and life form of the upper stratum (Table 1). The structure of the community and the species therein reflect the amount of moisture available to the plants e.g. tall dense plant communities are found in high rainfall areas whereas more stunted open communities occur in drier regions. Edaphic factors also influence the eventual structural formation.

The majority of *Ramalina* collection locations lie in those plant communities listed on the top left hand side of Table 1, representing those which occur in relatively high rainfall areas and have

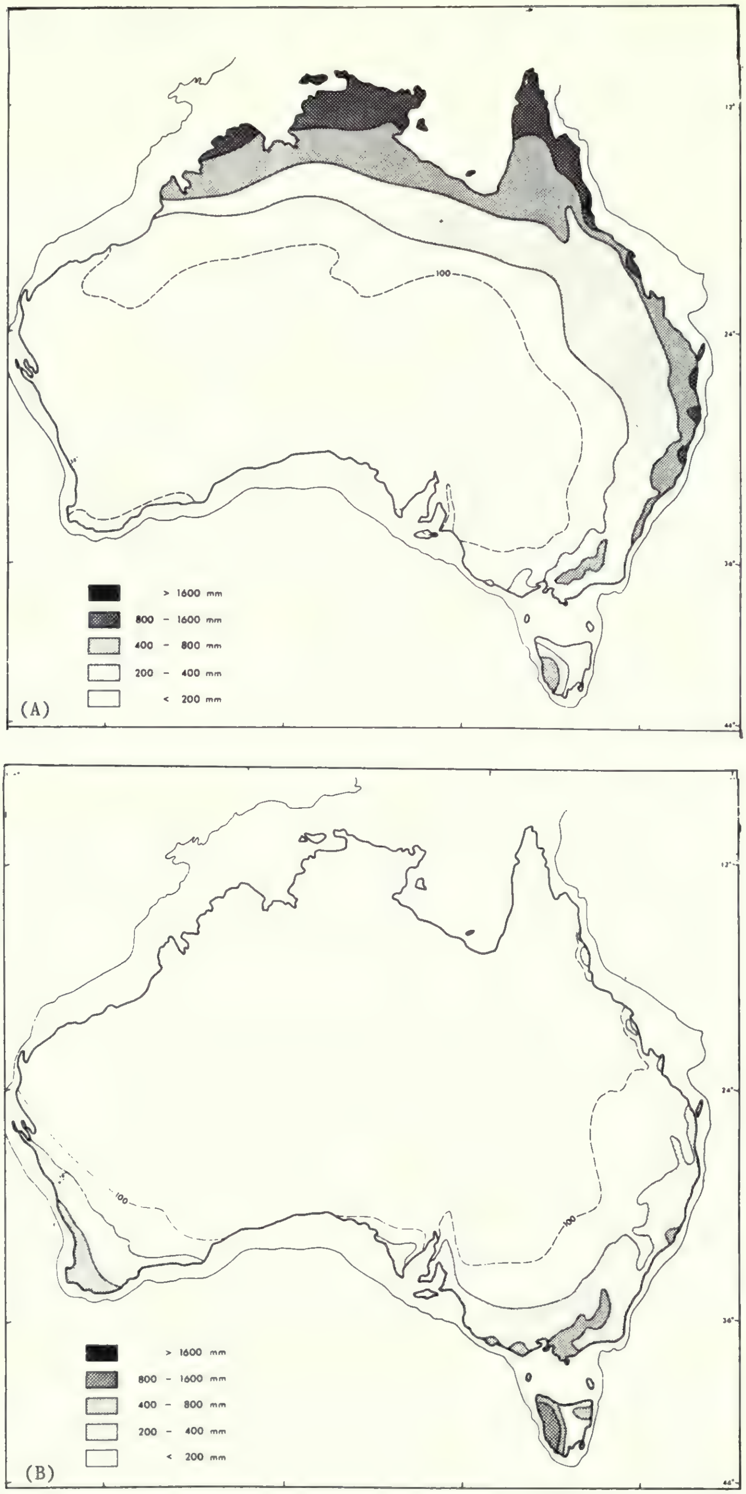
100
12°
24°
36°
44°
> 1600 mm
800 - 1600 mm
400 - 800 mm
200 - 400 mm
< 200 mm
(A)
100
100
12°
24°
36°
44°
> 1600 mm
800 - 1600 mm
400 - 800 mm
200 - 400 mm
< 200 mm
(B)

Fig. 2 A. Summer seasonal rainfall (November–April) equalled or exceeded 8 years in 10; B. Winter seasonal rainfall (May–October) equalled or exceeded 8 years in 10 (adapted from Nix, 1981).

Table 1 Structural formations in Australian plant communities (modified from Specht, 1970).

	Foliage projective cover of tallest stratum				
Life form of tallest stratum	100–70%	70–50%	50–30%	30–10%	<10%
Trees >30 m	Tall closed-forest	Tall open-forest	—	—	—
Trees 10–30 m	Closed-forest	Open-forest	Open-forest	Woodland	Open-woodland
Trees <10 m	Low closed-forest	Low open-forest	Low open-forest	Low woodland	Low open-woodland
Shrubs >2 m	Closed scrub	Open-scrub	Open-scrub	Tall shrubland	Tall open-shrubland
Shrubs 0·25–2 m					
Heathy	Closed-heathland	Open-heathland	Open-heathland	Low shrubland	Low open-shrubland
Chenopodiaceous	—	—	Low shrubland	Low shrubland	Low open-shrubland
Shrubs <0·25 m	—	—	—	Dwarf open-heathland	Dwarf open-heathland
Hummock grasses	—	—	—	Hummock grassland	Open hummock grassland

a relatively high Foliage Projective Cover (FPC) e.g. (1) Closed-forest, (2) Tall open-forest, (3) Open-forest, and (4) Open-scrub. These structural formations are made up of overstorey and understorey vegetation, and depending on the amount of canopy cover, vary in FPC from 100% to 30%. They can be briefly described as follows:

(a) *Closed-forest* (also referred to as rain-forest, it can also describe some mangrove forests). This community comprises many different tree genera and species which alter in composition with change in latitude. It is found in disjunct pockets from Cape York to Tasmania and grades from tropical mesophyll vine forests (with leaf size 45–180 cm^2) to subtropical mesophyll and notophyll vine forest (with leaf size 20·25–45 cm^2) to warm temperate notophyll vine forest to cool temperate microphyll moss forest (with leaf size 2·25–20·25 cm^2).

Closed-forest communities occur in humid areas where rainfall exceeds 1500 mm per annum; overstorey FPC in such a formation approaches 100%. These formations reach their best development on the basaltic soils of the Eastern Highlands. Several species of *Ramalina* grow in this habitat, two species are specific to the rain-forest canopy, and another three species are found in both closed-forest and open-forest communities.

These closed-forests can contain trees which exceed 30 m in height, but in monsoonal northern Australia and coastal Queensland, low closed-forests occur which are composed of trees reaching less than 10 m in height. During the wet season these forests have a FPC of 100%, but during the dry winters the FPC may be as low as 70% as some of the trees are semi-deciduous. In inland Queensland the low closed-forest is the only formation which supports any *Ramalina* species.

(b) *Tall open-forest* (with sclerophyllous understorey with or without tree ferns) occurs in sub-humid sites of eastern, south-eastern and south-western Australia. Overstorey FPC in such a community varies from 70% to 50%. The dominant tree species in the overstorey is *Eucalyptus*, whereas the low tree/tall shrub stratum (less than 10 m high) contains 18 genera of angiosperms (Specht, 1981*a*). Several species of *Ramalina* have been found growing on twigs in the understorey, but rarely do species of *Ramalina* grow on eucalypts.

(c) *Open-forest* (with either heathy sclerophyll or grassy understorey). This formation is the most widespread in Australia, occurring in the north, east, and southern parts of the continent; each area experiences quite different rainfall patterns ranging from summer rains to summer-winter uniform rainfall, to winter rains respectively. The genus *Eucalyptus* dominates these communities, although species of *Casuarina* and *Acacia* are also plentiful. The overstorey FPC for open-forest communities varies between 70–30%. No *Ramalina* species grow in the tropical open-forests, but occur on *Casuarina* and *Acacia* in the temperate communities.

(d) *Mallee open-scrub* (with savannah-chenopod understorey). This structural formation is common in the drier Mediterranean climate of southern Australia where species of *Eucalypt* dominate, but other genera, including *Acacia* are scattered between the mallee eucalypts. Overstorey FPC in these areas can be as low as 30%. The relatively low rainfall (250–800 mm p.a.) occurs in winter, followed by hot dry summers. Four species of *Ramalina* have been collected in this formation.

Seral plant communities exist along the coastal fringe of Australia; these are coastal dune communities and saline coastal communities, the latter made up of salt-marsh, mangrove vegetation, and marine meadow (Specht, 1981*a*); only the coastal dune community and the mangroves act as phorophytes for *Ramalina* species. Such communities usually produce a series of structural formations, influenced by micro-habitat conditions; the overstorey FPC therefore differs in different parts of the community.

(A) *Coastal dune community:* In the tropics, lowland rain-forest abuts the open coastline in areas where mangroves are not dominant; in the subtropics the sand dune vegetation comprises various shrub species of *Banksia integrifolia, Callitris columellaris*, and *Casuarina equisitifolia* as the dominant tree species. Along the southern coast-line, the foredunes are vegetated by heathy shrubs; *Pimelea serpyllifolia*, *Leptospermum laevigatum*, *Leucopogon parviflora*, *Monotoca elliptica*, *Bursaria spinosa*, and *Acacia sophorae*. Several *Ramalina* species occur in this community, the species varying with change in latitude and longitude.

(B) *The mangroves* (saline coastal community): This vegetation occupies the muddy areas at the mouths of rivers and bays along the eastern, north-western, and northern coastlines of Australia, with pockets in South Australia. The structure of such communities varies from closed-forest to woodland to tall shrubland. The major concentration of mangrove vegetation (approx. 28 species) is confined to the tropics gradually dwindling in species numbers in the subtropics and eventually being reduced to one species, *Avicennia marina*, towards the temperate zone. Both FPC and the amount of rainfall vary considerably depending on the latitude of the mangrove community.

Those mangrove species which act as phorophytes to the Ramalinae are *Rhizophora stylosa, Rhizophora apiculata, Ceriops tagal, Bruguiera gymnorhiza, Avicennia marina, Aegiceras corniculatum, Lumnitzera racemosa,* and *Excoecaria agallocha*.

(4) *Geology*

The saxicolous species of *Ramalina* are totally dependent on the presence of rock outcrops within their distribution range. Corticolous species, however, are only indirectly influenced through the presence or absence of particular plant communities which grow on the different soil types.

The four main rock types involved in the areas where *Ramalina* species occur are (1) basaltic rocks (2) metamorphics and fine grained sedimentary rocks (3) sandstones and (4) granites.

The major areas of basalt are Tertiary in age, and are confined to the Eastern Highlands. Most of these elevated areas are forested with either rain-forest or tall open-forest. Additional areas of basalt of Quaternary age are found in north-east and central-east Queensland, supporting low closed-forests, and western Victoria at lower altitudes on the coastal plain which supports extensive areas of open-woodland and grassland.

In eastern Australia the metamorphic rocks and many fine-grained, compacted sedimentary rocks which are associated with them are of Palaeozoic age, and have been folded and elevated, forming mountain ranges and hilly country in the Eastern Highlands. They have been intruded by granite batholiths, which also make up large areas, having been revealed by prolonged erosion e.g. New England, Murrumbidgee, Kosciusko, and many other masses in the eastern states. These are areas of high elevation subject to cold winters.

The sandstones which are most important are those sub-horizontal deposits of Mesozoic age forming for example, much of the surface of the Sydney Basin, Moreton Basin, and the Carnarvon Range. The Grampians are composed of dipping sandstones of Palaeozoic age.

In South Australia and Western Australia only a few species of *Ramalina* occur on trees growing on soils derived from old granites and metamorphic rocks (schists and quartzites). There are very few occurrences of Ramalinae in areas of calcareous rocks of the Tertiary basins and Pleistocene dune deposits.

Historical understanding of *Ramalina* and Ramalinaceae

(1) THE GENUS *RAMALINA*

The genus *Ramalina* was first described by Acharius (1810) when he distinguished it from *Parmelia* by its cartilaginous thallus and apothecial characters.

Acharius (1810) listed ten species (together with their forms) as belonging to the genus, namely *Ramalina homalea, R. linearis, R. complanata, R. peruviana, R. polymorpha, R. fraxinea, R. fastigiata, R. scopulorum, R. farinacea*, and *R. pollinaria*. Except for the first, all of these species have been retained in the genus to the present day.

Many more taxa have been added to this original number in the last 175 years, some being removed later into separate genera because of differences found in the anatomy, the spore shape and size, or the colour of pycnidia. Montagne (1852) examined the cortex of *R. homalea* Ach. and found that the hyphae were arranged perpendicular to the surface without any mechanical support tissue in the cortex; he therefore erected a new genus *Desmazieria* Mont. to incorporate all *Ramalina* species possessing this anatomical feature, using *R. homalea* as the type.

Massalongo (1854) erected the genus *Cenozosia* Massal. based on *R. inanis* Mont. as the type and characterized by its fistulose spongy thallus with a single layer of branching cells in the cortex. This monotypic genus has been retained as a distinct taxon up to the present.

By using the colour of spermatia, as well as anatomical and thallus differences, Stizenberger (1862) divided the genus *Ramalina* into three parts (i) *Cenozosia* (Massal.) (type *R. inanis* Mont.) as a species with thallus hollow, spermatia black (ii) *Desmazieria* (Mont.) (type *R. ceruchis* Ach.) for those species with simple cortex, thallus interior cottony and spermatia black and (iii) *Euramalina* Stizenb. (type *R. scopulorum* Retz.) for species having a double cortex, thallus interior cottony, and spermatia pale or colourless.

Nylander (1870) also used colour of spermogonia conceptacles for initial division within the genus, separating species with (1) totally black spermatia (2) partially black or (3) pale or colourless spermatia. Within group (1) he then used differences in anatomical structure of the cortex to separate *R. inanis* Mont. (= *Cenozosia* Massal.) from the rest. He placed five other species in another group which corresponds to *Desmazieria* Mont., namely *R. ceruchis* Ach., *R. combeiodes* Nyl., *R. homalea* Ach., *R. flaccescens* Nyl., and *R. testudinaria* Nyl.

Ramalina melanothrix Laurer was separated from the rest because of its two-layered cortex (= *Euramalina* Stizenb.); its present position is in the genus *Trichoramalina* Rundel & Bowler. Group (2) contained only *R. carpathica* Körber, a species which Bowler & Rundel (1977) placed in the genus *Fistulariella* Bowler & Rundel. Group (3) contained 56 species which today belong in three genera, *Ramalina* Ach., *Niebla* Rundel & Bowler, and *Fistulariella* Bowler & Rundel.

Vainio (1890) also laid stress on anatomical structure of the cortex, accepting section *Euramalina* Stizenb. as having a chondroid cortex made up of longitudinal hyphae, and sections *Desmazieria* (Mont.) and *Cenozosia* (Massal.) as having a cortex made up of transverse hyphae. Vainio divided *Euramalina* Stizenb. into two stirps based on thallus structure (1) *Fistularia* Vainio species with inflated hollow branches and (2) *Myelopoea* Vainio species with a continuous arachnoid or cottony medulla. He used branch shape to subdivide stirps *Myelopoea* into series *Teretiusculae* Vainio (containing species with terete or angular branches) and series *Compressiusculae* Vainio (containing species with flattened branches rarely two-edged).

Hue (1901) followed Vainio in this division of *Ramalina* when he divided the genus into three groups on morphology: (A) *Teretiusculae* Vainio (B) *Compressiusculae* Vainio and (C) *Fistulosae* Hue.

Steiner (1904) based his divisions of *Ramalina* on the arrangement of cortical tissue external to the algal layer. His section *Corticatae* (outer layer consisting of more or less transversely arranged conglutinated hyphae) was equivalent to *Desmazieria* Mont., his section *Bitectae* (outer layer as above overlying a tissue of longitudinally arranged conglutinated hyphae) was similar to *Euramalina* Stizenb. He made a third division *Ecorticatae* (cortex composed of a layer of longitudinally oriented conglutinated hyphae which formed a closed ring). *Ramalina arabum* (Ach.) Meyen & Flotow is the type for *Ecorticatae*. Choisy (1954) commented that this thallus structure was similar to *Alectoria* Ach.

Howe (1913–14) used spore characters to distinguish the sections he created within the genus *Ramalina* as he thought this represented a more natural classification. Section *Ellipsosporae* R. H. Howe contained species with ellipsoid or oblong spores (9–20 × 3·5–7·5 μm) and section *Fusisporae* R. H. Howe contained species with long fusiform spores (16–35 × 3–7 μm) and section *Bistortae* R. H. Howe contained a species with sigmoid spores.

Each of these sections he divided into series and these series correspond in the main with previous divisions, e.g. Howe's series *Desmazieria* (Mont.) = section *Corticatae* Steiner = genus *Niebla* Bowler & Rundel. Series *Myelopoeae* = part of *Myelopoea* Vainio, series *Fistulariae* = stirps *Fistularia* Vainio = genus *Fistulariella* Bowler & Rundel. He made three other series, *Tenuicorticate, Ciliate,* and *Fusisporae*. This classification is not used.

Du Rietz (1926) relegated the genus *Desmazieria* Mont. to subgenus *Desmazieria* (Mont.) (containing *R. ceruchis, R. homalae,* etc.) and *Euramalina* Stizenb. to subgenus *Euramalina* (Stizenb.), which he divided into section *Tenuicorticatae* R. H. Howe and section *Bitectae* Steiner. Section *Tenuicorticatae* contained species without a chondroid element and this section he further divided into subsection *Solidae* Du Rietz (species with a solid thallus, containing *R. evernioides,* etc.) and subsection *Tubulosae* Du Rietz (species with inflated fistulose thallus: *R. inanis* Mont. = *Cenozosia* Massal.).

Du Rietz maintained section *Bitectae* Steiner (= *Euramalina* Stizenb.) but divided it into two subsections (a) subsection *Myelopoea* Vainio thallus solid, and (b) subsection *Fistularia* Vainio thallus inflated, fistulose. These extra subsections make the classification complicated although the basic criteria used for division are sound.

Zahlbruckner (1907) combined the sections of both Stizenberger (1862) and Steiner (1904) and made three divisions in the genus *Ramalina*: (i) section *Ecorticatae* Steiner (ii) section *Corticatae* Steiner (which incorporated *Cenozosia* Massal. and *Desmazieria* Stizenb.) and (iii) section *Euramalina* Stizenb. (= *Bitectae* Steiner). Zahlbruckner subdivided *Euramalina* Stizenb. using the Vainio names *Fistularia* Vainio and *Myelopoea* Vainio and series *Teretiusculae* Vainio and *Compressiusculae* Vainio.

Present day taxonomists are still divided in their acceptance of which species should be placed in the genus *Ramalina* sens. str. Bowler & Rundel (1977) established the new genus *Fistulariella* Bowler & Rundel for those species originally placed in *Ramalina* stirps *Fistularia* Vainio. They placed emphasis on the hollow, usually perforate thallus as traits warranting genus status, yet Australian material belonging to stirps *Fistularia* Vainio present a broad range of morphology varying from almost totally compressed to totally fistulose. It is therefore regarded here that the trait of inflation of the thallus should have no greater emphasis placed upon it than the roundness of branches.

Rundel & Bowler (1978) proposed a new generic name *Niebla* to replace the genus name *Desmazieria* Mont. as they found the former name was a homonym for the earlier described genus *Desmazeria* Dumortier (Poaceae), and 13 taxa were transferred by them from *Desmazieria* and *Ramalina* into *Niebla* Rundel & Bowler.

Of the various divisions put forward up to the present day, the taxonomic system used by Vainio would most suitably classify the Australian material, e.g. the Australian Ramalinae would broadly divide into three groups: (1) fistulose thalli (2) terete and solid thalli and (3) compressed and solid thalli.

(2) THE FAMILY RAMALINACEAE

Agardh (1821: 93) erected the family Ramalinaceae ['Ramalineæ'], in which he placed the genus *Ramalina*. Since that time the genus has been alternatively included with *Usnea* and other fruticose genera in the family Usneaceae, or isolated in the family Ramalinaceae. Table 2 shows the various classifications which record *Ramalina* in Ramalinaceae (with or without other members of Usneaceae) and the diversity of opinions as to the position of the genus.

Apparently Zahlbruckner (1907) and Smith (1921) did not regard septate spores nor a cortex with mechanical tissue sufficiently different to separate *Ramalina* from other genera in the family Usneaceae; but Watson (1929) regarded spore septation as most important and placed *Ramalina* in the Ramalinaceae.

With modern day improvement in techniques of microscopy and chemistry together with a better understanding of the fungal/algal composition, the natural relationships which exist between the genera are being more fully understood.

Follmann & Huneck (1969) placed three genera in the family Ramalinaceae based on their chemotaxonomy and anatomy (viz. *Ramalina, Ramalinopsis*, and *Desmazieria*). Poelt (1974) also regarded these three genera as forming a natural entity and placed them in Ramalinaceae, but he added a fourth genus which was not closely related, e.g. *Speerschneidera*. Culberson & Culberson (1970) pointed out that chemical evidence supported segregation of Ramalinaceae as a separate family as no species in the Usneaceae proper produces orcinol meta-depsides, a category of substances richly represented in *Ramalina*.

Henssen & Jahns (1973) have kept the genus *Ramalina* in the family Ramalinaceae, because of its two-celled spores and exobasidial conidiophores, and because of the specific lichen substances it contains. They stated that the structure of the apothecium of *Ramalina* resembles that of the Parmeliaceae in that there is a more or less complete algal layer beneath the hymenium, but the Ramalinaceae differ from the characteristic cupular exciple of the Parmeliaceae in that the algal layer is next to, not separated from the loosely interwoven subhymenium.

Keuk (1979) divided the genera in Ramalinaceae into two groups based on anatomical and chemical differences, and colour of pycnidial walls (a) *Ramalina, Ramalinopsis,* and *Trichoramalina* and (b) *Niebla* (= *Desmazieria* Mont. and *Cenozosia* Massal.).

The most modern division within the family Ramalinaceae has been based on cortical diversity. Bowler (1981) defined seven genera in the Ramalinaceae: *Ramalina* Ach., *Fistulariella* Bowler & Rundel, *Niebla* Rundel & Bowler, *Ramalinopsis* (Zahlbr.) Follm. & Huneck, *Trichoramalina* Rundel & Bowler, *Dievernia* M. Choisy, and *Cenozosia* Massal. Of these, the genus *Ramalina* contains the largest number of taxa.

It can be seen from Table 2 that all recent authors who have specifically dealt with the question of relationships of genera within the two families Ramalinaceae and Usneaceae, have considered them to be distinct morphologically, chemically, and taxonomically.

Collectors of Australian Ramalinae

Because the early explorers in Australian waters sailed in the temperate latitudes, it was only to be expected that the first *Ramalina* collected in Australia would be a temperate region species; this collection was made by Labillardière, a botanist on the French ship 'Recherche' which sailed along the Great Australian Bight and visited Tasmania in 1791 (Ducker, 1979). This first specimen, held at H, (H-NYL 37226) was annotated '*Ramalina leiodea* Nyl. Labillardiere, C. van Dieman'. This was an erroneous identification which has now been determined as *R. inflata* J. D. Hook. & Taylor.

In 1802, Robert Brown in his voyages with Matthew Flinders collected *R. inflata* from Port Jackson (Sydney, N.S.W.), but this specimen was determined as *Lichen fastigiatus* Ach. by Crombie (1880).

When J. D. Hooker accompanied Sir James Ross in his Antarctic expedition in the ships 'Erebus' and 'Terror' in 1839, he collected the type of *R. inflata* J. D. Hook. & Taylor on the Lord Auckland Islands and from New Zealand he collected the type of *R. geniculata* J. D. Hook. & Taylor. They also visited Tasmania and collected material which was later published in *Flora Tasmaniae* (1859). In this work Churchill Babington cites *R. tasmanica* Nyl. as a new species but

Table 2 The classification of genera within the two families Ramalinaceae and Usneaceae as proposed by various lichenologists from 1814 to the present day.

Author	Date	Class/Order	Tribe/Family	Genus
Acharius, E.	1814	Class Homothalami		
		Order Primus	Scutellati	*Ramalina, Alectoria, Collema*
		Order Secundus	Peltati	*Usnea, Cornicularia*
Agardh, C.	1821		Ramalineae	*Ramalina*
Eschweiler, F. G.	1824		Usneaceae	*Usnea, Ramalina, Alectoria* ± *Cornicularia, Dactylina, Desmaziera, Endocena, Evernia, Everniopsis, Letharia, Neuropogon, Oropogon, Siphula, Thamnolia.*
Montagne, J. F. C.	1852		Tr. Parmeliacea	
			subtribe Usnea	*Ramalina, Usnea*
Nylander, W.	1857	Lichenacei		
		Ser. Ramalodei	Tr. Ramalinei	*Ramalina, Alectoria, Evernia, Dufourea, Dactylina*
			Tr. Usneei	*Usnea, Neuropogon, Chlorea*
Stizenberger, E.	1862	Class Homothalami	Tr. Usneaceae	
			Ramalineae	*Ramalina, Dactylina, Cetraria, Evernia, Dufourea*
			Usneaceae	*Usnea, Alectoria, Oropogon, Argopsis*
Vainio, E. A.	1890	Order Cyclocarpeae	Tr. Parmelieae	*Ramalina, Usnea, Alectoria, Evernia*
Hue, A. M.	1901	Series Cyclocarpae	Radiatae	
			Tr. Ramlineae	*Ramalina, Dufourea*
			Tr. Usneae	*Usnea*
			Tr. Alectoreae	*Alectoria*
Zahlbruckner, A.	1907	Order Cyclocarpeae	Usneaceae	*Ramalina, Usnea, Alectoria, Oropogon, Dufourea, Evernia, Everniopsis, Endocena, Letharia, Thamnolia, Siphula, Dactylina.*
Smith, A. L.	1921	subseries Cyclocarpineae	Usneaceae	*Ramalina, Usnea, Alectoria, Evernia, Letharia, Everniopsis, Oropogon, Thamnolia, Siphula, Dactylina, Dufourea, Endocena*
Watson, W.	1929	Order Parmeliales	Ramalinaceae	*Ramalina*
			Usneaceae	*Usnea, Alectoria, Letharia, Evernia, Everniopsis, Dactylina, Dufourea, Thamnolia, Siphula, Endocena*
Räsänen, V. J. P. B.	1943	Order Cyclocarpeae	Usneaceae	*Ramalina, Usnea, Alectoria, Evernia, Letharia, Everniopsis, Dufourea, Dactylina, Oropogon, Ramalea*
Choisy, M.	1957		Ramalinaceae	*Ramalina*
			Usneaceae	*Usnea, Desmazieria, Cenozosia*

Table 2 – *cont.*

Author	Date	Class/Order	Tribe/Family	Genus
Follmann, G. & Huneck, S.	1969		Ramalinaceae	*Ramalina, Ramalinopsis, Desmazieria*
Henssen, A. & Jahns, H. M.	1973	Order Lecanorales suborder Lecanorineae	Ramalinaceae	*Ramalina*
Poelt, J.	1974	Order Lecanorales suborder Lecaniorieae	Ramalinaceae Usneaceae	*Ramalina, Ramalinopsis, Desmaziera, Speerschneidera,* *Usnea, Alectoria, Bryopogon, Cornicularia, Evernia, Everniopsis, Himantormia, Letharia, Sulcaria, Neuropogon, Oropogon*
Bowler, P. A.	1981		Ramalinaceae	*Ramalina, Fistulariella, Trichoramalina, Niebla, Dievernia, Cenozosia, Ramalinopsis*

examination of this material during the present study has shown this specimen to be yet another morphotype of the very variable *R. inflata*.

The Reverend Dr. W. Woolls, a school master at Parramatta, N.S.W., in 1832, collected in that area, and one *Ramalina* specimen called *R. gracilis* Nyl. (MEL 9432) is actually *R. exiguella* Stirton.

During the period 1842–46, J. P. Verreaux (a French ornithologist) who was sent to Australia by the Museum of Natural History in Paris, collected widely in Tasmania and mainland Australia. In his botanical collections were several *Ramalina* species which he had obtained during that period, either by collecting them himself or by purchase of material from others (Lamy, in litt.). Because of this practice of obtaining specimens from other collectors there is uncertainty about the locality given by Nylander for two 'type' specimens he records as collected by Verreaux from Swan River, Western Australia, these are *R. australiensis* Nyl. and *R. confirmata* Nyl. Both of these species grow in eastern Australia, and the Western Australian types are the only material collected from that area. Nylander himself appeared unsure of the locality of *R. australiensis* as he noted: 'in Australia (prope Swan River, ni fallor) legit Verreaux 1846'. Verreaux collections held at PC indicate he travelled north as far as Moreton Bay, Queensland, and collected several *Ramalina* species from mangroves.

The first woman recorded as a lichen collector was Amalie Dietrich, who collected lichens in Queensland for a wealthy Hamburg merchant named Godeffroy, for his private museum. Some of these collections are now housed at München. They are collections of *Ramalina* species from the Rockhampton area.

Friedrich Ludwig Leichhardt travelled through Queensland on his way to Port Essington (Darwin), 1844–45. He collected a *Ramalina* (now *R. filicaulis* N. Stevens) along the way but gave no exact location. As the occurrence of this species is rare today, more information about the locality would have been helpful in the present study.

Ferdinand von Mueller, Victorian Government Botanist (1853–96), received lichen specimens from various collectors in Australia and these specimens were sent to overseas lichenologists for determination, e.g. Anton Krempelhuber, Jean Müller [Arg.], and James Stirton.

Daniel Sullivan, a headmaster, collected lichens for von Mueller, one being the 'type' of *R. glaucescens* Krempelh., from Mt Ararat, western Victoria, and another was *R. leiodea* var. *fastigiatula* Müll. Arg. 'type' from the Grampians. Another *Ramalina* which Sullivan collected from Mt Ararat area (MEL 9471) now bears the name *R. fimbriata* Krog & Swinscow, a species common in East Africa. Charles French, a plant propagator at Melbourne Botanical Gardens

(Filson, 1976), collected the type of *R. inflata* var. *fissa* Müll. Arg. from King Island, Bass Strait. The type of *R. lacerata* Müll. Arg. was collected at Eucla, Western Australia, by J. Oliver.

Collectors in New South Wales for the Victorian Botanical Department included T. White who collected the type of *R. myrioclada* Müll. Arg. from Twofold Bay, New South Wales. Charles Knight, a New Zealand surgeon, collected lichens in the Sydney area; he named one specimen *R. subgeniculata* C. Knight, which was subsequently changed to *R. knightiana* Zahlbr. Knight also named *R. minuscula* var. *alba* a specimen collected by James Keys at Mt Perry, Queensland. This name was published by Bailey (1886), but no description was given and later John Shirley (1888) described it.

Messrs. Pentzke and Hartmann were two collectors in Queensland for the Victorian Botanical Department (Wilson, 1889). Pentzke collected the type material of *R. farinacea* var. *nervulosa* Müll. Arg. from Daintree River, north Queensland, and C. H. Hartman of Toowoomba collected the type material of *R. geniculata* var. *compacta* Müll. Arg.

Collections made by F. M. Bailey, Government Botanist in Queensland, John Shirley, a school inspector, and Mrs M. Thozet, were sent to James Stirton, W. Leighton, Charles Knight, or Jean Müller [Arg.] for identification (Wilson, 1889). It was Stirton who named the two *Ramalina* types *R. exiguella* Stirton and *R. perpusilla* Stirton. Müller Arg. described a Rockhampton specimen collected by Mrs Thozet as *R. farinacea* var. *squarrosa* Müll. Arg. The type of *R. farinacea* var. *dendroides* Müll. Arg. was collected by E. Forde from the Hunter River, New South Wales. Both of these taxa have now been found to be morphotypes of *R. peruviana* Ach.

The Reverend F. R. M. Wilson, from Kew, Victoria, collected prolifically (1877–97) in eastern Australia, from Tasmania to Brisbane, and more particularly along Port Phillip Bay and Gippsland, Victoria (Filson, 1976). He collected the type of *R. calicaris* var. *australica* Räsanen from Barwon Heads. Wilson himself described several taxa of *Ramalina*, e.g. *R. unilateralis* F. Wilson, *R. brevis* F. Wilson, and *R. brevis* var. *brevissima* F. Wilson.

More recent collectors of Ramalinae in Australia are J. H. Willis, Assistant Government Botanist at the National Herbarium Melbourne (Filson, 1976), A. C. Beauglehole, who collected Ramalinae in South Australia and Victoria, J. S. Whinray, who made an extensive survey of the lichen flora of the Bass Strait Islands, and G. C. Bratt and J. A. Cashin, whose collections of Tasmanian lichens have proved invaluable in the present study.

Other present day lichenologists who have collected *Ramalina* specimens which have been used in the present study are A. Archer (N.S.W.), J. A. Elix (A.C.T.), R. Filson (Vic.), G. Kantvilas (Tas.), R. W. Rogers (Qld.), N. Sammy (W.A.), C. Scarlett (Qld), and R. Seppelt (S.A.).

Materials and methods

The source of material for this research was threefold. (a) Personal collections (numbering over 10,000 specimens), the majority from Australia, with small collections from the Pacific Islands of Fiji, New Caledonia, Rarotonga, Tahiti, New Hebrides, New Zealand, and Hawaii. (b) Herbarium material from institutes, as acknowledged. (c) Herbarium and living material from private collections, as acknowledged.

Most of the specimens examined during this study were tested by thin-layer chromatography using the techniques of Culberson (1972). Solvents B and C proved to be the most useful solvents to separate the acids found in the various species of *Ramalina*. The chemistry of type material was also checked. Examination of the surface features of the thallus (e.g. pseudocyphellae, soralia, and soredia shapes) and spore size and shape, was carried out by use of the Scanning Electron Microscope (SEM) using either a Cambridge or a Phillips 505. In order to observe the shape and thickness of the hyphae composing the outer cortex and the supportive tissue thin sections were examined by TEM, using an AEI Corinth 275 operated at 60 kV. Preparation of thallus material involved fixation of the tissue in glutaraldehyde, post fixation in osmium tetroxide, dehydration and then infiltration and embedding with Spurrs medium. The results were not always successful as the tissue tended to pull away from the medium along the outer cortex junction.

All climatic data were derived from Meterological Bureau records (*Climatic averages of Australia*, 1975).

Results

Morphology

(a) *Soralia and soredia:* Soralia are defined herein as those areas of thallus where clusters of soredia are found, and the term soredia is applied to the more or less spherical bodies composed of algae surrounded by short hyphae which act as vegetative diaspores. These vegetative reproduction bodies are produced by 11 of the Australian Ramalinae, and their constancy in occurrence enables this attribute to be used taxonomically.

The position and form of the soralia are also useful criteria in the separation of each sorediate taxon. Round or ellipsoid soralia are produced by *R. pacifica, R. caespitella, R. nervulosa* var. *nervulosa, R. nervulosa* var. *luciae*, and *R. nervulosa* var. *dumeticola* (Plate 1, fig. 3); these occur marginally and laminally. *Ramalina peruviana* and *R. tenella* produce small, punctiform soralia (Plate 1, figs 1, 2) which are mainly apical in *R. tenella* and marginal or lateral in *R. peruviana*. The soralia found in the other four taxa are produced in several ways, e.g. (i) by disintegration of the lower cortex (*R. fimbriata*, Plate 1, fig. 5) (ii) by the partial separation, both marginally and apically, of the upper and lower cortices (*R. canariensis*) (iii) by lack of a continuous lower cortex (*R. reducta*, Plate 1, fig. 4) and (iv) by the splitting or disintegration of parts of the lower cortex at intervals along the branches (*R. unilateralis*, Plate 1, fig. 6). The soralia terminology used by Du Rietz (1924) and Beltman (1978) was not generally applicable to the Ramalinae.

The composition of the soredia was examined under SEM; the algal cells were not discernable but the fragments of hyphae which make up the outer surface of the soredium were observed to differ in form in several of the taxa. The northern hemisphere species *R. capitata* is regarded as having soredia covered by an 'epicortex-like' layer (James, pers. comm.) (Plate 2, fig. 1), and such a structure was looked for in the Australian sorediate taxa. Four species were found to possess some semblance of an outer covering (Plate 2, figs 2, 3, 4, 5). Whether this layer should be compared to the 'epicortex' which occurs in some taxa in the Parmeliaceae as described by Hale (1973, 1981) is debatable; but it can be likened to the 'Kittsubstanz' (cementing substance) mentioned by Peveling (1970). Such a layer may act as a protection against wetting of the soredia.

The Australian taxa which produce soredia with this outer covering are *R. caespitella, R. reducta, R. tenella,* and *R. fimbriata*, and even in these only a minority of the soredia show it clearly. The soredia of *R. caespitella* are small, spherical, and have a partially smooth surface (Plate 2, fig. 2). Soredia of *R. reducta* are irregular in shape and size but fusion of the external hyphal segments was apparent (Plate 2, fig. 3). *Ramalina tenella* soredia are small but well defined, and some have a distinct outer covering (Plate 2, fig. 4). *Ramalina fimbriata* soredia are

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Plate 1 (*overleaf*) SEM photographs showing soralia shapes in some of the Australian Ramalinae. Fig. 1 Apical, punctiform soralia – *R. tenella*. Scale 10 mm = 530 μm (× 19). Fig. 2 Marginal/lateral, punctiform soralia – *R. peruviana*. Scale 10 mm = 150 μm (× 65). Fig. 3 Round and ellipsoid soralia – *R. nervulosa* var. *dumeticola*. Scale 10 mm = 220 μm (× 44). Fig. 4 Exposed lower surface with chondroid strands of cortical tissue across area of soralia – *R. reducta*. Scale 10 mm = 270 μm (× 36). Fig. 5 Patches of exposed medulla by disintegration of the under side – *R. fimbriata*. Scale 10 mm = 200 μm (× 51). Fig. 6 Lower surface split apart and eroded at intervals – *R. unilateralis*. Scale 10 mm = 530 μm (× 19).

Plate 2 (*overleaf*) SEM photographs showing soredia forms in some of the Australian Ramalinae. Scale indicated by black bar. Fig. 1 *R. capitata* – showing smooth outer layer partially covering the soredium. Scale 10 mm = 22 μm (× 440). Fig. 2 *R. caespitella* – showing portion of soredia covered by a smooth layer. Scale 10 mm = 22 μm (× 440). Fig. 3 *R. reducta* – showing soredia with smooth surface (× 364). Fig. 4 *R. tenella* – showing thin layer partially enclosing the soredium (× 1236). Fig. 5 *R. fimbriata* – showing thin layer totally enclosing soredium (× 958). Fig. 6 *R. unilateralis* – showing soredium with a 'woolly' appearance; no outer layer present (× 1527). Fig. 7 *R. nervulosa* var. *dumeticola* – showing soredia with irregular surface (× 873). Fig. 8 *R. canariensis* – showing soredia with a 'woolly' appearance; no outer layer present (× 909).

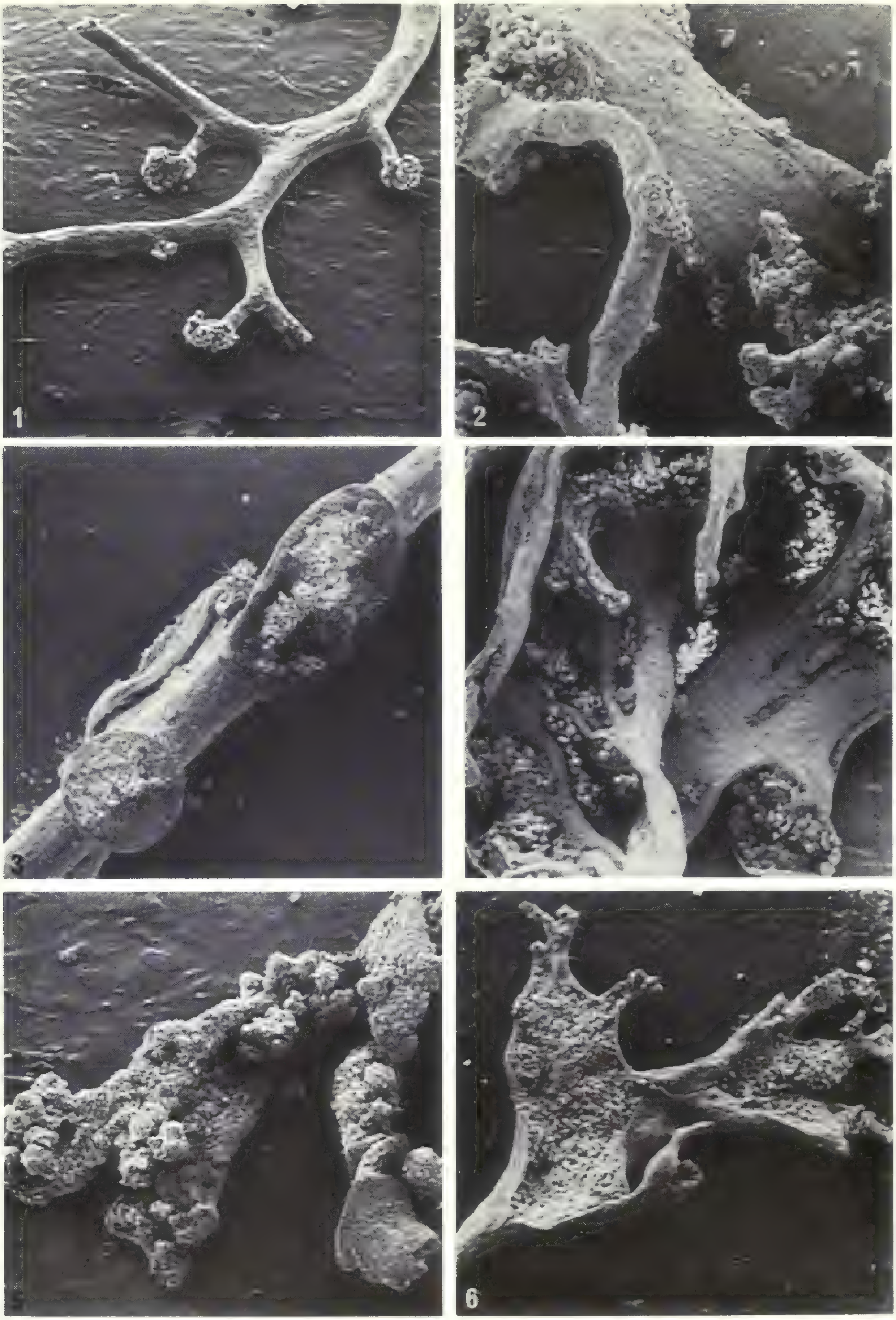
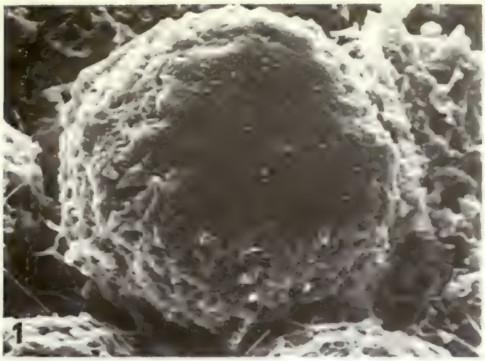
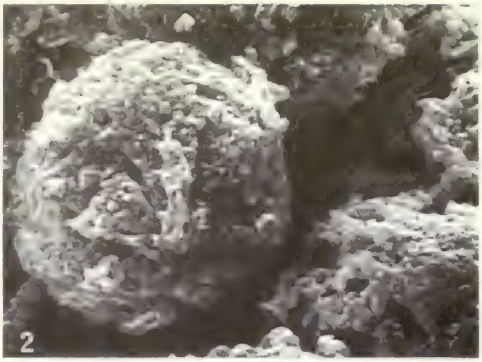
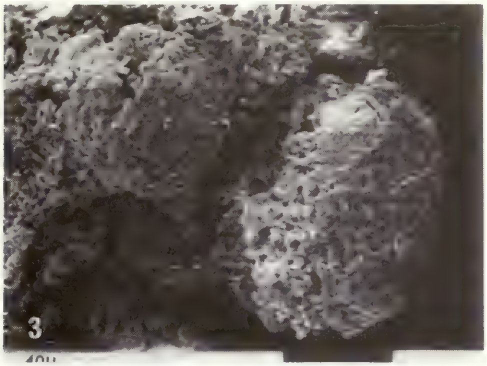
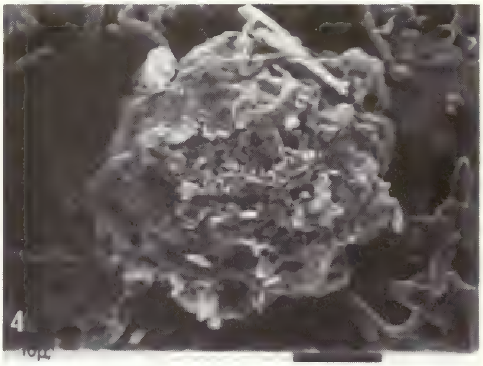


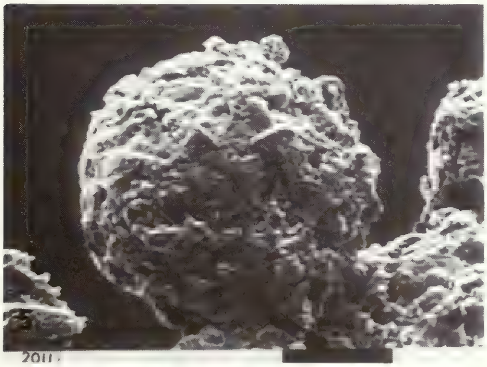
Plate 1

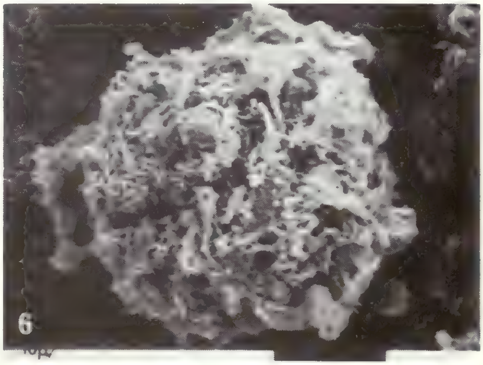


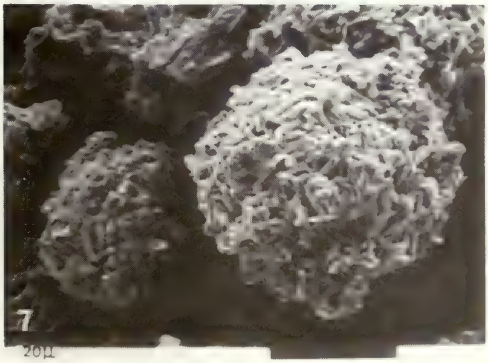












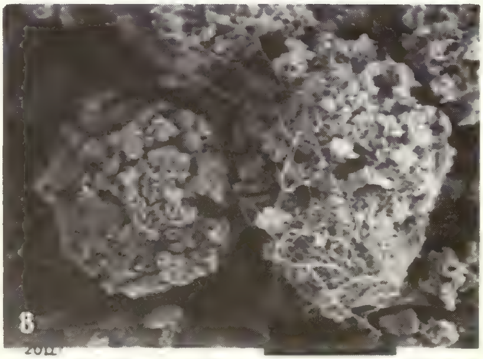


Plate 2

large and spherical, and the formation of an external layer could be discerned on many of the soredia at various stages of development; the most advanced layer formation is shown in Plate 2, fig. 5. All of these taxa are regarded as having granular soredia.

The soredia produced by *R. unilateralis* (Plate 2, fig. 6) and by *R. canariensis* (Plate 2, fig. 8) are small in size and are composed of both thick and thin pieces of hyphae; there is no external fusion of the hyphae so the outer surface remains loosely interwoven giving a woolly appearance to the soredia (Plate 2, fig. 6). The soredia are farinose. The four taxa which belong in the *R. farinacea* complex (*R. pacifica, R. nervulosa* var. *nervulosa, R. nervulosa* var. *luciae*, and *R. nervulosa* var. *dumeticola*; Plate 2, fig. 7; Plate 3, figs 1, 2, 3) also produce soredia which have an irregular surface made up of separate hyphal pieces which are not fused (Plate 3, fig. 2), and the soredia are farinose. *Ramalina peruviana* produces soredia which have an irregular surface (Plate 3, fig. 4).

Fibrils often arise from mounds of farinose soredia (Plate 1, fig. 2) and these features have the same structure as the soredia (Plate 3, fig. 7).

(b) *Apothecia:* The production of apothecia as a sexual means of reproduction occurs in all but four of the Australian Ramalinae (i.e. seven of the 11 sorediate taxa also produce apothecia, but only rarely, and often the mature ascospores are few and difficult to find). The esorediate taxa generally produce numerous apothecia.

The position of the apothecia on the branches can be of taxonomic importance, being terminal, subterminal, marginal, lateral, or laminal. Terminal refers to the apothecia at the end of a branch. Subterminal refers to apothecia positioned near the end of the branch, with the branch extending beyond the apothecium, forming a short attenuate branchlet or spur, which is usually bent at an angle in relation to the main branch. If the spur grows long it makes the branch appear geniculate. Marginal refers to apothecia on the edges of compressed branches, and laminal refers to apothecia occurring on the surface of the thallus. If branches are subterete to terete the apothecia occur laterally. When laminal apothecia occur specifically at the base of bifurcating branches they are referred to as positioned at the axil of the branch.

Apothecial shape varies from concave to plane to convex; in some species the apothecia remain concave to maturity, in others the apothecia are concave to plane when immature, but are markedly convex at maturity. The thalline margin is usually distinct and entire, occasionally becoming incised at maturity; when the disc becomes convex the margin is often obscured.

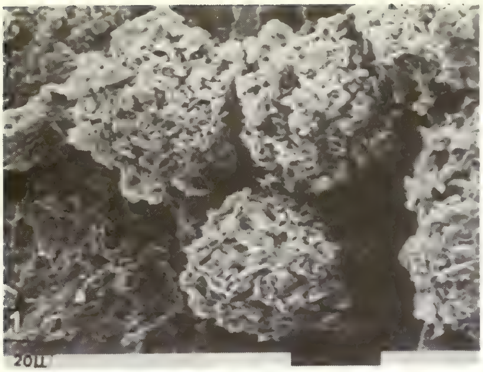
The size of the apothecia varies greatly from 0·2 mm to 5·0 mm with exceptions to 10 mm. Most apothecia are shortly stalked, but sessile apothecia are found in *R. australiensis* and *R. filicaulis*. The colour of the disc is usually yellow-green and pruinose; however, taxa in the *R. celastri* complex have been found with orange coloured discs.

The apothecial tissue comprises a colourless hymenium formed of asci and paraphyses. The asci are clavate to subcylindrical and lie amongst sparsely branched paraphyses over a developed hypothecium. This hypothecial layer is usually brownish-yellow as is the epithecium [as used in a lichenological context – Henssen & Jahns (1973)].

(c) *Spores:* The number of spores per ascus is eight, usually distichous in arrangement (Plate 5, fig. 5), hyaline, 1-septate, varying considerably in size and shape, being broadly ellipsoidal to fusiform and either straight to slightly curved or reniform (Plates 4 & 5).

Within a single ascus spores can vary from straight to curved, a feature also noted by Krog &

Plate 3 SEM photographs showing soredia forms and surface features in some of the Australian Ramalinae. Scale indicated by black bar. Fig. 1 *R. nervulosa* var. *luciae* – showing soredia with irregular surface (× 750). Fig. 2 *R. nervulosa* var. *nervulosa* – showing fragments of hyphae making up the outer surface, without a surface layer (× 945). Fig. 3 *R. pacifica* – showing soredia with an irregular surface (× 525). Fig. 4 *R. peruviana* – showing soredium with an irregular surface (× 1300). Fig. 5 Punctiform pseudocyphellae – *R. subfraxinea* var. *confirmata* (× 75). Fig. 6 Enlargement of section of Fig. 5 (× 750). Fig. 7 Fibril produced from a mound of soredia – *R. peruviana*. Scale 10 mm = 30 μm (× 341). Fig. 8 Tuberculate pseudocyphellae – *R. subfraxinea* var. *subfraxinea*. Scale 10 mm = 30 μm (× 341). ▶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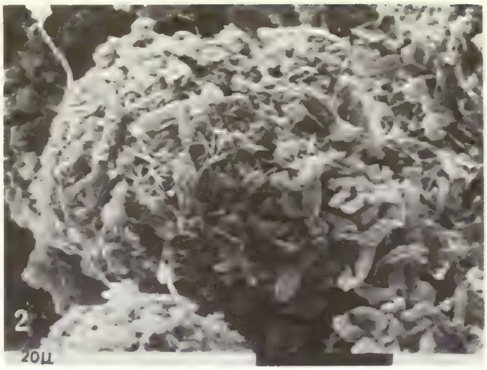
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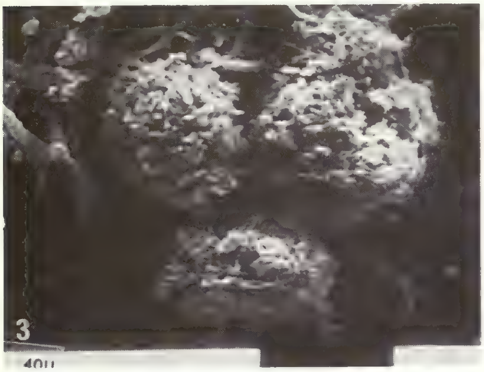
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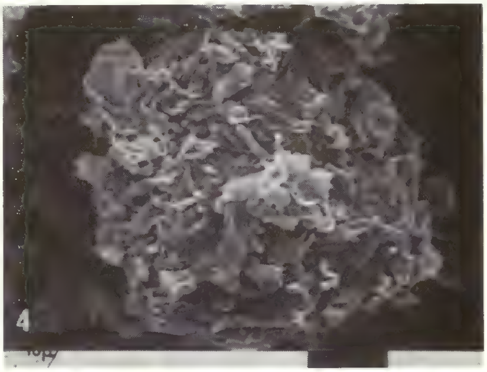
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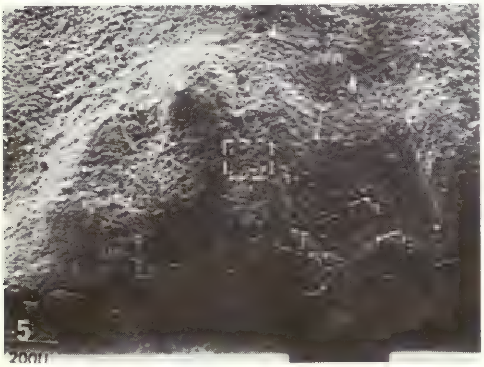
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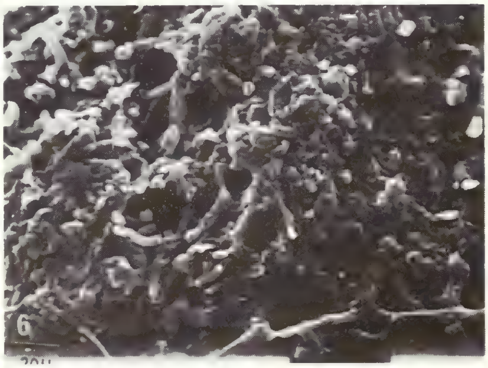
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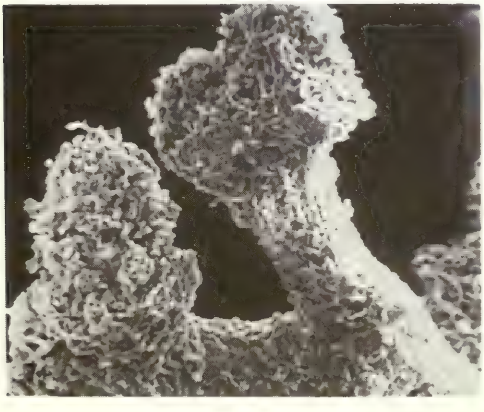

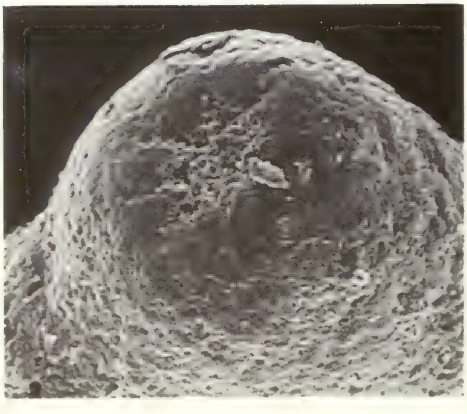

Swinscow (1975) and Landrón (1972) (Plate 4, fig. 4); therefore the shape of spores was not used as a taxonomic character. The size of spores has also been found to be of limited taxonomic value as most mature spores of the *Ramalina* species lie within the size range (8–)10–16 × 3·5–6 μm (Plate 4, figs 2, 3, 4, 5, 6). The relationship between the width and length of spores, as suggested by Krog & Swinscow (1974) was investigated in this study to see if this could be a taxonomic tool for separation of closely related taxa; however exceptions could always be found in the spore ratios which negated the usefulness of this characteristic (Plate 5, figs 2, 3, 4).

Although the spores are 2-celled, some of the spores in the size range 14–16 × 4μm appear 3 or 4-celled. These additional divisions are not produced by distoseptae so must be dense cytoplasmic strands (which take up the cotton blue stain) across the cell which produce a 'mock septation'.

The spores of each taxa examined under SEM showed surfaces which were remarkably smooth (Plates 4 & 5) except for a film which seemed to coat some of the spores or remained in patches attached to the spore surface (Plate 4, fig. 1; Plate 5, figs 1, 2, 4, 6).

(d) *Pycnidia:* The occurrence of pycnidia amongst the Australian *Ramalina* species is not common. When present, they are always pale in colour, and produce pycnoconidia which are rod-shaped, usually 3·5 × 0·5 μm in size. It was observed that they mainly occurred on sterile thalli rather than on thalli bearing either apothecia or soredia. This suggests that they may provide an alternative means of propagation for the species. Their irregular occurrence and apparent uniformity prevented their taxonomic use.

(e) *Pseudocyphellae:* Many lichenologists have discussed these morphological characters (Du Reitz, 1924; Culberson & Culberson, 1968; Duncan, 1970; Beltman, 1978; Bowler, 1981; and Hale, 1981). It is generally accepted that these features are cortical pores in the surface of the thallus which allow the exchange of gases. They are areas which have direct contact with the medullary hyphae. In the Ramalinae they vary in shape and size and several names have been applied to such surface features: striae, striations, tubercules, and papillae.

Pseudocyphellae appear as shallow depressions (striae) in the cortex (Plate 3, figs 5, 6) or as white linear markings (striations) on the surface (Stevens, 1983*a*: figs 1B–D, 2A–B). In the *Ramalina subfraxinea* complex in Australia some of the taxa produce tubercles resembling raised warts, the tips of these structures containing small pseudocyphellae (Plate 3, fig. 8). The term 'tuberculate pseudocyphellae' was used by Krog & Swinscow (1975) to describe this form of pseudocyphellae. Similar surface features occur in several North American taxa, but are referred to as papillae, as in *R. sinaloensis* (Bowler & Rundel, 1972*b*) and *R. complanata* (Landrón, 1972).

Most sorediate *Ramalina* species produce pseudocyphellae of one kind or another; in the case of the *R. farinacea* taxa from the tropics, it was found that the elongate pseudocyphellae were precursors to soralia formation (Stevens, 1983*a*).

Bowler (1981) reported that pseudocyphellae are mainly absent in the *Fistulariella* taxa and this was found to be so in the Australian fistulose material. As a diagnostic character for the separation of taxa, pseudocyphellae have been found to be of little value.

Anatomy

The anatomical structure of all *Ramalina* species found in Australia comprises (1) a cortex (which I regard as both the outer cortex plus the inner supportive tissue) and (2) a medulla (which includes the phycobiont).

Plate 4 SEM photographs showing spore shapes in the Australian Ramalinae. Fig. 1 *R. subfraxinea* var. *leiodea* – single spore. Scale 10 mm = 1·2 μm (× 8000). Fig. 2 *R. australiensis* spores. Scale 10 mm = 4 μm (× 2400). Fig. 3 *R. pacifica* spores. Scale 10 mm = 4 μm (× 2400). Fig. 4 *R. subfraxinea* var. *confirmata* spores. Scale 10 mm = 4 μm (× 2400). Fig. 5 *R. subfraxinea* var. *norstictica* spores. Scale 10 mm = 4 μm (× 2400). Fig. 6 *R. subfraxinea* var. *subfraxinea* spores. Scale 10 mm = 4 μm (× 2400).

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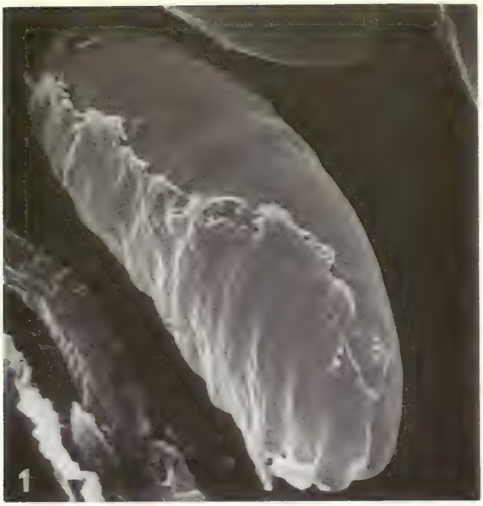
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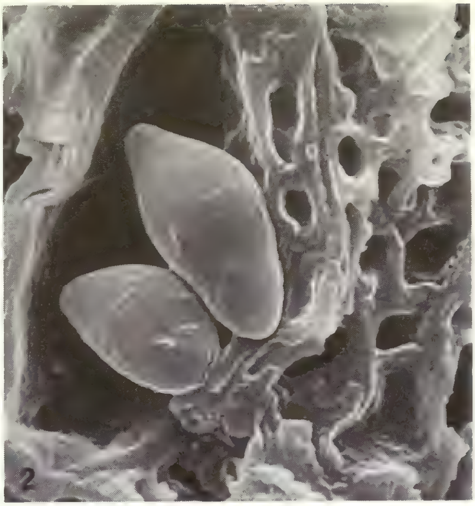
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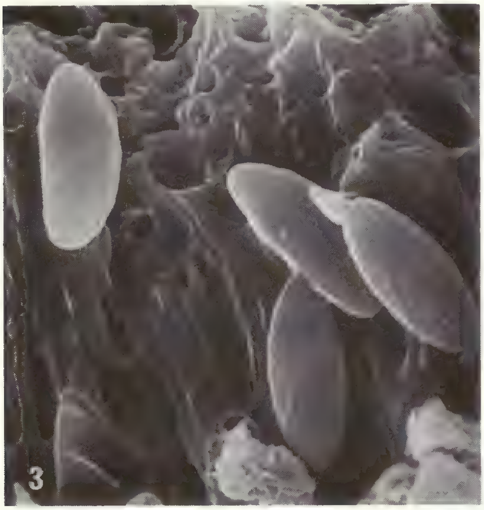
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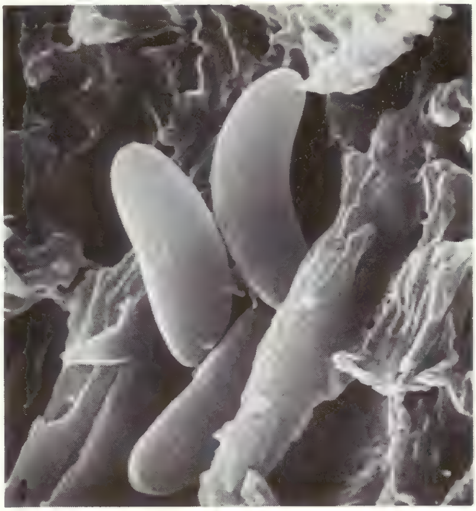

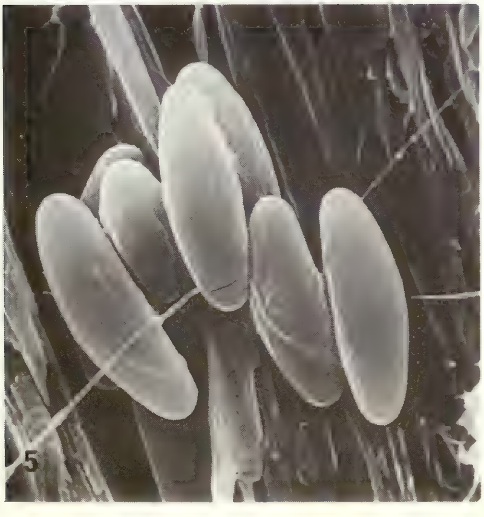
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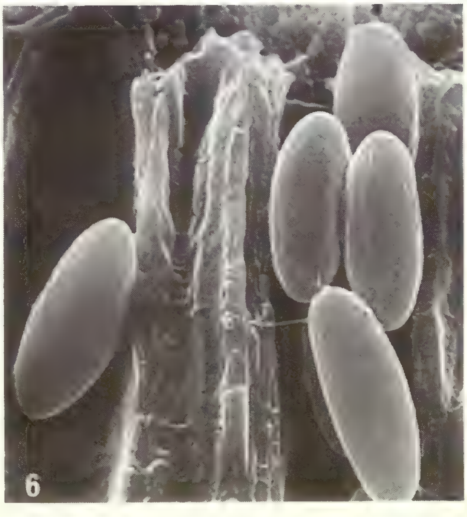
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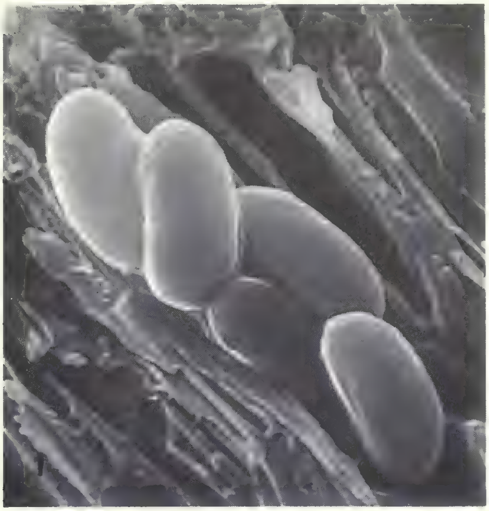
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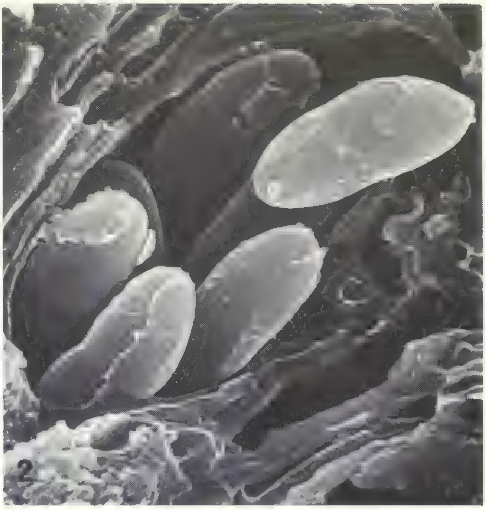
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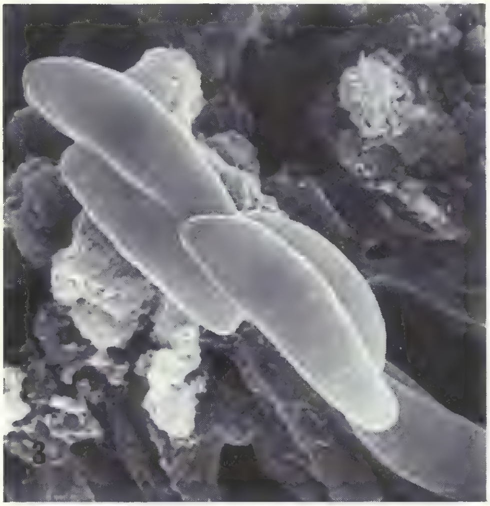
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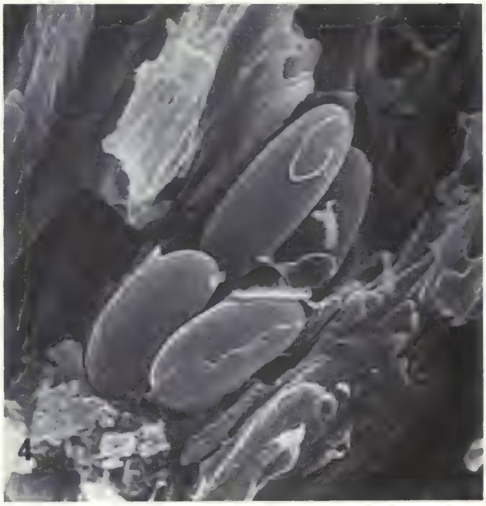
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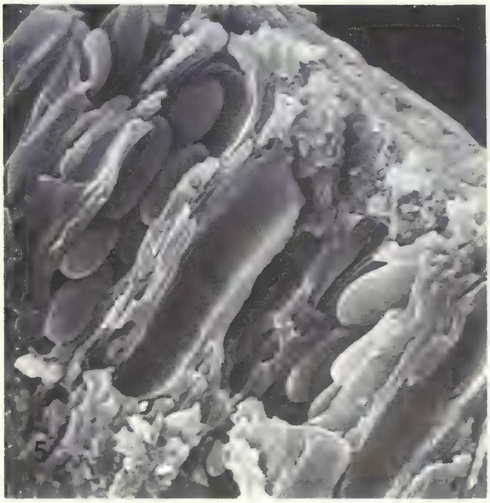
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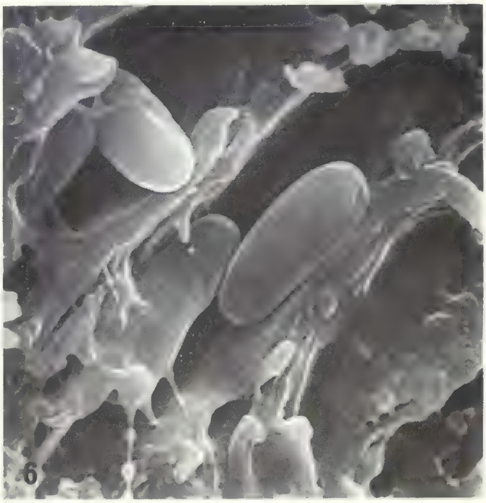
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(1) *Cortex*

In the Australian taxa the outer cortical layer is usually 20 μm in thickness and is composed of thick walled, transverse or randomly oriented hyphae; it may be indistinct or even absent. The inner layer serves as supportive tissue and varies in thickness. It is composed of bundles of more or less periclinally arranged thick walled hyphae which make up a continuous or interrupted sheath around the internal medullary hyphae.

The detail in the outer cortex is often difficult to detect under light microscopy when yellowish granules are present; a problem pointed out by Bowler (1981). To obtain as much detail as possible, sections were examined under TEM. Both cortical layers of hyphae are highly gelatinized and a uniform distribution of lumina is apparent; each lumen is surrounded by a thick matrix of fibrillar material arranged concentrically (Plate 6, fig. 1). Peveling (1974) commented that it is difficult to determine whether the different layers around hyphae are part of the proper cell wall or if they are extracellular additions to the wall.

The change in orientation of the hyphae is apparent under TEM. In transverse section the randomly orientated outer layer hyphae appear elongate whereas the longitudinally oriented hyphae appear circular (Plate 6, fig. 2). Scattered between the hyphae are outlines of crystals, which are more dense in the outer region and may be usnic acid crystals (Plate 6, fig. 3).

(a) *Anatomical structure as a means of separating taxa.* Krog & Østhagen (1980) divided the species of *Ramalina* found in the Canary Islands into four anatomical types based on the position of the supportive tissue: the *farinacea* type, the *decipiens* type, the *bourgaeana* type, and the *duriaei* type. The latter two types occur in species now placed in the genera *Niebla* and *Dievernia* and are therefore not relevant to Australian material.

The majority of the Australian Ramalinae could be classed as belonging to the *farinacea* type (Figs 3A, B), as they possess a thin outer layer of tissue and a continuous inner layer of mechanical tissue of uneven thickness. Variations can occur in the arrangement of this inner supportive tissue if it becomes partly discontinuous, leaving sections of outer tissue unsupported (Fig. 3C). However, this is not comparable with the '*decipiens* type' where some of the strands anastomose across the medulla. None of the Australian taxa could be separated on this trait.

Bowler (1981) pointed out that the *Ramalina* taxa could be divided arbitrarily into two groups based on the degree of specialization in the cortical tissue. One group with a narrow, indistinct outer cortex intergrading with the underlying supportive tissue and the other group with a distinctly double-structured cortex, but he commented that intergradation could be seen between the two forms.

The Australian taxa can be divided in this way generally, but thalli within one taxon can often show differences in thickness of the outer cortical layer. Those taxa with a sparse or indistinct outer cortex are *R. caespitella, R. celastri* complex, *R. pacifica, R. nervulosa, R. exiguella* (Plate 6, fig. 4), *R. peruviana, R. reducta*, and *R. unilateralis.* Those taxa with a comparatively distinct double-structured cortex are *R. australiensis, R. canariensis, R. filicaulis, R. fimbriata, R. glaucescens, R. inflata* complex, *R. litorea, R. subfraxinea* complex (Plate 6, fig. 5), and *R. tenella.*

(b) *Variation in the anatomical structure within the thallus.* It was noticed when serial sectioning thalli that differences in anatomical structure sometimes occurred depending on the portion of the branch cut. Two forms of variation were found. The first form of variation is (i) variation in the alignment of the hyphae in the supportive tissue in basal sections compared to the hyphal arrangement in the mid and apical sections. Basal sections of *R. celastri* subsp. *ovalis* show a typical thin outer cortex merging with the longitudinally oriented hyphae in the supportive tissue, as found in the anatomy of *R. celastri* subsp. *celastri* (Plate 6, fig. 7). Sections cut through the middle of the branch and towards the apex showed only a wide band of randomly oriented

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◀ **Plate 5** SEM photographs showing spore shapes in the Australian Ramalinae. Fig. 1 *R. exiguella* spores. Scale 10 mm = 4 μm (× 2400). Fig. 2 *R. inflata* subsp. *inflata* spores. Scale 10 mm = 4 μm (× 2400). Fig. 3 *R. inflata* subsp. *perpusilla* (inland taxon) spores. Scale 10 mm = 4 μm (× 2400). Fig. 4 *R. inflata* subsp. *perpusilla* (coastal taxon) spores. Scale 10 mm = 4 μm (× 2400). Fig. 5 *R. celastri* subsp. *celastri* spores within the ascus. Scale 10 mm = 8·3 μm (× 1163). Fig. 6 *R. litorea* spores. Scale 10 mm = 4 μm (× 2400).

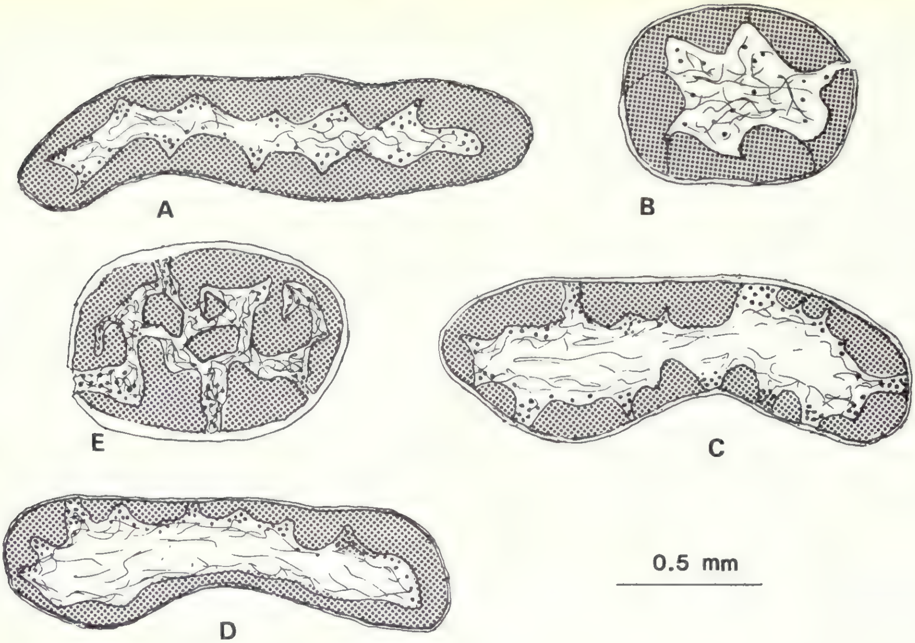


Fig. 3 Anatomical structures of Australian *Ramalina* thalli: A. Cross section showing uneven thickness of supportive tissue in typical '*farinacea*-type' anatomy; B. Cross section of *R. filicaulis* terete branch showing typical '*farinacea*-type' anatomy; C. Cross section of *R. inflata* subsp. *perpusilla* thallus showing variation from Fig. A – the supportive tissue being partly discontinuous; D. Algal clusters on the upper side only, as found in some thalli of the *R. inflata* group; E. Cross section of *R. whinrayi* showing thick outer cortex and irregular arrangement of supportive tissue which extends into the medullary region, with isolated rafts of supportive tissue also present.

hyphae forming a network (Plate 6, fig. 6). This anomaly may be explained by the number of laminal apothecia that this taxon produces on both sides of the branch. The lack of supportive tissue and the random arrangement of hyphae could be due to the repeated formation of apothecial tissue from the middle of the branch to the apex. Brandt (1906) found that variations occurred within a single thallus, and illustrated this with serial sections along the branch of *Ramalina curnowii*.

The second form of variation is (ii) variation in cortical structure between the upper side of the branch and the lower side. This was noticed by Brandt (1906) in the species *R. populina*. In Australian material such variation was found to occur in some specimens of *R. inflata* subsp. *inflata* and *R. inflata* subsp. *perpusilla*, where the inner cortex on the lower side is narrow, continuous and of even thickness, without an algal layer, but on the upper side it is partly discontinuous, of uneven thickness with algal clusters interspersed between the ridges (Fig. 3D). This formation appears to be a modification of the normal '*farinacea* type' structure, to enable optimal functioning of the phycobiont under particular environmental conditions. It is not a constant feature of these taxa, so cannot be used taxonomically.

Another taxon which has an atypical and complex anatomy (Fig. 3E) is *R. whinrayi*. The cortex consists of a thick outer cortex and a thick, discontinuous sheath of supportive tissue made up of bundles with ridges extending across the medulla or occurring as isolated rafts in the medulla; such intrusions produce islands of medullary tissue with algal clumps. This form of anatomy has been sighted in the northern hemisphere taxon *R. capitata* (= *R. strepsilis*).

(2) *Medulla*

The central portion of the thallus is occupied by medullary hyphae which are randomly oriented, either tightly compacted or loosely woven and arachnoid. In the fistulose taxa the hyphae may be

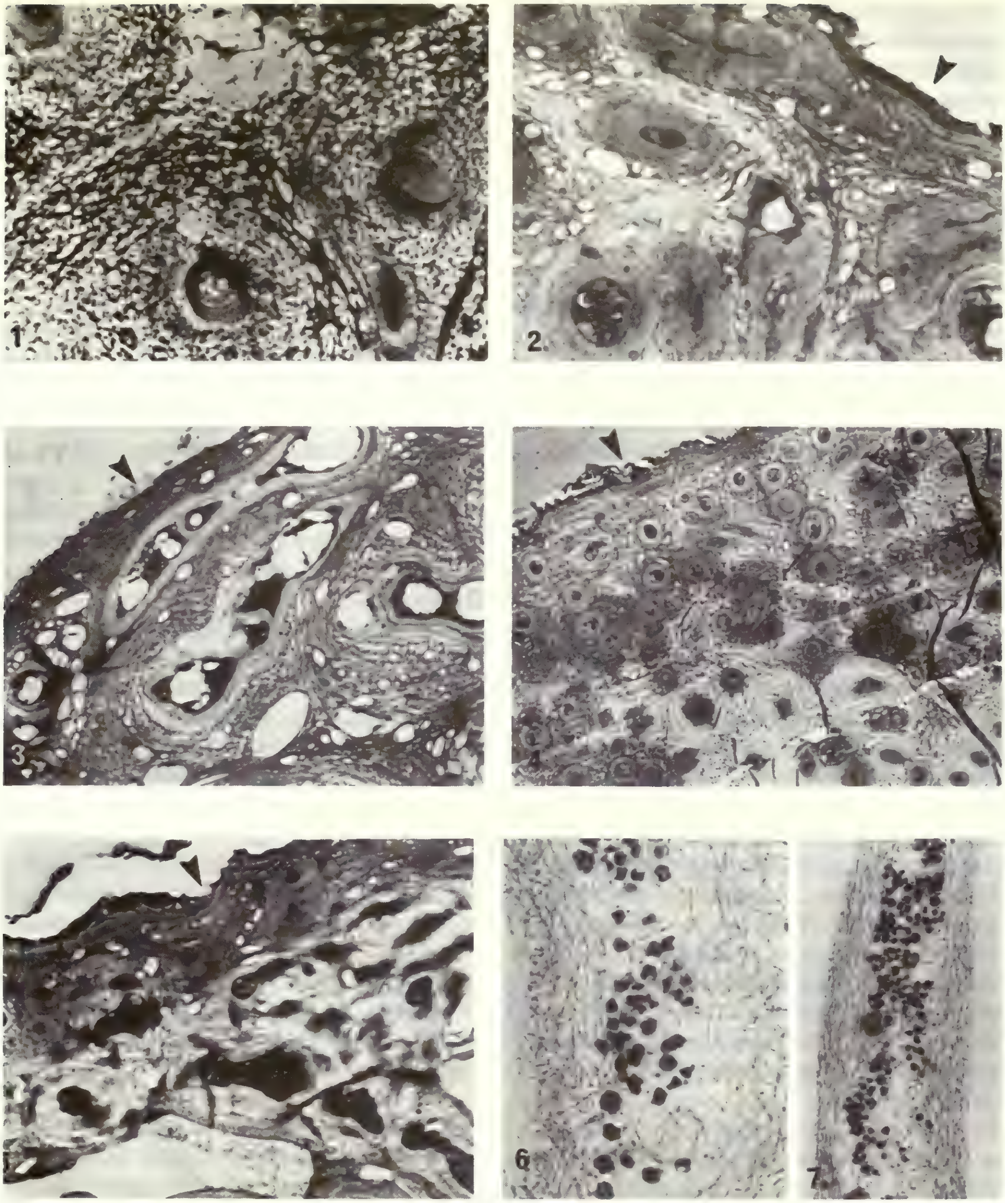


Plate 6 TEM photographs showing anatomical features. External edge of outer cortex indicated by black arrow. Fig. 1 Lumen with surrounding fibrillar matrix. Scale 10 mm = 1·5 μm (× 6770). Fig. 2 Section from outer to inner cortex – *R. exiguella*. Scale 10 mm = 1 μm (× 10450). Fig. 3 Usnic acid? crystals in outer cortex – *R. peruviana*. Scale 10 mm = 1·8 μm (× 5682). Fig. 4 Section from outer to inner cortex showing narrow outer cortex. Scale 10 mm = 5 μm (× 2125). Fig. 5 Section from ouer to inner cortex showing broad outer cortex. Scale 10 mm = 1·2 μm (× 5000). Fig. 6 L.S. of mid-section of branch of *R. celastri* subsp. *ovalis*. Scale 1 mm = 10 μm (× 105). Fig. 7 L.S. of mid-section of branch of *R. celastri* subsp. *celastri*. Scale 1 mm = 19 μm (× 53). (Photographs for Figs 6 & 7 by courtesy of A. Henssen.)

almost totally lacking, or occur in patches appressed to the inner cortex. *Ramalina fissa* produces very little medullary hyphae, whereas in some *R. inflata* subsp. *inflata* specimens the central cavity is criss-crossed by arachnoid hyphae to the same degree as *R. glaucescens*, a species regarded as having a solid, compressed thallus.

The sorediate species belonging to the *R. farinacea* group in Australia have a thick felty medulla compared to the *R. farinacea* taxa in the northern hemisphere which have a loosely compacted but continuous medullary layer. Other sorediate species, *R. canariensis, R. fimbriata, R. reducta,* and *R. unilateralis,* reveal large areas of exposed medulla which produce soralia. The most compacted medullary hyphae are found in *R. whinrayi* (Fig. 3E).

Chemistry

Usnic acid is found in the cortex of the Ramalinae in varying amounts but it is not used taxonomically as a diagnostic property. Atranorin occurs only rarely and in trace amounts so it is not used for taxonomic purposes either. It is the medullary substances produced by the Ramalinae – the depsides and the depsidones – which are important.

(a) *The orcinol depsides:* These comprise both *para-* and *meta*-depsides. The *para*-depside divaricatic acid is particularly common and is found in ten Australian *Ramalina* species. It may occur as the sole medullary constituent or be accompanied by biogenetically closely related accessory acids such as stenosporic acid, nordivaricatic acid (both *para*-depsides) or by sekikaic acid (a *meta*-depside).

Evernic acid, another *para*-depside occurs in one saxicolous species endemic to Australia, and lecanoric acid has been found as an accessory acid in this species. Evernic acid is rare in southern hemisphere Ramalinae, whereas in the northern hemisphere it is a relatively common constituent in this genus.

The greatest number of lichen acids found in the Australian Ramalinae belong to the orcinol *meta*-depside group. Fourteen substances have been identified in this study. The most common metabolite is sekikaic acid which is found in nine species. In marked contrast it is found in only a few northern hemisphere *Ramalina* species. Sekikaic acid may occur as the sole medullary constituent or be accompanied by a number of minor acids viz. homosekikaic, ramalinolic, 4'-0-demethylsekikaic, 4'-0-methylnorhomosekikaic, and 4'-0-methylnorsekikaic acids.

Cryptochlorophaeic acid is another orcinol *meta*-depside which has been observed alone or may occur accompanied by paludosic and 4'-0-methylcryptochlorophaeic acids. Boninic acid too, occurs as a major acid with the minor metabolites 2-0-methylsekikaic, 2,4'-di-0-methylnorsekikaic, 4'-0-methylpaludosic, and 4,4'-di-0-methylcryoptochlorophaeic acids (Chester & Elix, 1978).

(b) *The β-orcinol depsidones:* Only four β-orcinol depsidones have been observed in Australian Ramalinae. Salazinic acid is present in four species and may be accompanied by trace amounts of protocetraric acid, but protocetraric acid does not occur as a major component in any of the species. Norstictic acid occurs in one coastal species and psoromic acid is present in one inland species.

The number of depsidones found in the Australian Ramalinae is less than the number found in *Ramalaina* species in Europe or North America, where fumarprotocetraric acid, hypoprotocetraric acid, stictic acid, protocetraric acid, norstictic acid, psoromic acid, and salazinic acid all occur.

Salazinic acid occurs in both sorediate and fertile *Ramalina* species which inhabit the Australian coastline (viz. *R. pacifica, R. tenella,* and *R. fissa*). In *R. pacifica* and *R. tenella* trace amounts of protocetraric acid are sometimes present accompanying the salazinic acid. The occurrence of these two acids in the same thallus is probably due to incomplete enzymic oxidation of the side chain methyl group in the conversion of protocetraric acid to salazinic acid (Elix, in litt.).

Triterpenoids, derived from the mevalonic pathway occur in specimens of *R. tenella*, and terpenes have been found in several species but neither of these groups was utilized for taxonomic purposes.

Chemical variation and species concept

Since the chemistry of a particular species is usually constant it has proved a useful property in combination with morphological characters to define a lichen species. However, in some instances, morphologically identical taxa are found to contain different acids and the problem arises of how to treat them taxonomically. Elix (1982) pointed out that there are three common patterns of chemical variation (a) replacement type compounds (b) accessory type compounds and (c) chemosyndromic variation.

(a) *Replacement compounds:* Replacement compounds occur in a number of Australian *Ramalina* taxa including *R. whinrayi, R. glaucescens,* the *R. inflata* complex, the *R. farinacea* complex, and the *R. subfraxinea* complex. The most common acids involved are divaricatic acid, sekikaic acid, and salazinic acid.

The thalli of *R. whinrayi* produce either divaricatic acid ± nordivaricatic acid or the replacement compound sekikaic acid with minor metabolites (4'-0-demethylsekikaic acid and trace amounts of 4'-0-methyl norhomosekikaic acid). On the Tasmanian coastline both of these races occur in the one population, their morphology is indistinguishable, and one thallus was found to contain both divaricatic and sekikaic acids.

On the Bass Strait islands only the divaricatic acid race occurs on the islands in the Hogans Group (the most northerly islands), whereas on the Kents Group of islands and on Craggy Island only the sekikaic acid race was found, although most thalli contain trace amounts of divaricatic acid as well. Because of this dual occurrence of the acids in some thalli, both acid races are regarded as belonging to the one taxon, viz. *R. whinrayi*.

An intensive study of the habitats in which each acid race occurs would be necessary to understand and interpret the segregation of the two acid races on the different islands. A survey similar to that carried out by Culberson (1969*a*) on taxa in the *R. siliquosa* complex may solve this problem if it could be found that the Tasmanian population occupied separate niches according to the acids present. In this case the chemical races could be regarded as taxonomically significant (Culberson, 1967, 1969*b*) and the explanation of the mixed acids would infer hybridization (Brodo, 1978). But the islands are small and inaccessible and such a survey was not possible during this study.

The occurrence of replacement compounds was also observed in the *R. inflata* group, where lichen populations which are morphologically indistinguishable may contain either divaricatic acid or sekikaic acid as medullary substances. Here again such taxa have been regarded as chemical strains within the species; a decision strengthened by the presence of trace amounts of sekikaic acid in some thalli which contain divaricatic acid. A third replacement compound, salazinic acid, also occurs in the *R. inflata* complex. Biogenetically this depsidone is quite remote from the two depsides, yet thalli possessing this acid are remarkably similar to those with a depside chemistry. However, the depsidone taxon has been retained as a separate species (*R. fissa*), as it has a geographically different distribution pattern from the depside containing taxa.

(b) *Accessory compounds:* Accessory type compounds are also present in the *R. inflata* complex, occurring sporadically in addition to the constant constituents, but having no correlation with any morphological or distributional variations (Elix, 1982). The presence of nordivaricatic acid in some divaricatic acid taxa and the presence of consalazinic or scabrosin derivatives in the salazinic taxon have been regarded as instances of accessory acids accompanying the major constituent and thus requiring no taxonomic recognition. Similarly the accessory acid connorstictic has been found in the norstictic acid taxon in the *R. subfraxinea* complex.

Another *Ramalina* species complex comprising taxa with chemical variants of the replacement type and with accessory compounds is the tropical/subtropical *R. farinacea* complex. The acids involved are divaricatic acid (+ accessory compound stenosporic acid) and the sekikaic aggregate of acids and salazinic acid, but this group is further complicated by chemosyndromic variation occurring within taxa which produce the sekikaic aggregate of acids.

(c) *Chemosyndromic variation:* A chemosyndrome is a group of biogenetically related metabolites where one or two compounds are regularly the major components, and the minor biosequentially related constituent of one taxon becomes the major constituent of the other (Culberson & Culberson, 1977; Elix, 1982).

In the *R. farinacea* complex, the two tropical/subtropical taxa *R. nervulosa* var. *luciae* and *R. nervulosa* var. *dumeticola* contain the same acid components but these occur in different quantities in each taxon (Stevens, 1983*a*).

Correlation between secondary-product chemistry and ecogeography in the *Ramalina subfraxinea* complex

The importance of chemistry in identifying taxa which have different amplitudes of ecological tolerance has been stressed by Culberson (1967, 1969*b*), Culberson & Culberson (1967), and Sheard (1978). The notable example of correlation between secondary-product chemistry and ecogeography is found in the *R. siliquosa* species complex of the northern hemisphere. This complex contains six sibling species each with a different depsidone chemistry (norstictic acid, salazinic acid, stictic acid, protocetraric acid, hypoprotocetraric acid, and acid deficient). Culberson (1969*b*) maintained that each chemical race was a different species which reflected the physiological differences between the taxa. However, the *R. siliquosa* chemistry comprises a replacement series of medullary depsidones which are able to be ranked by increasing numbers of oxidation steps in their biosynthesis (Culberson, Culberson & Johnson, 1977).

The maritime *R. subfraxinea* complex in the southern hemisphere is similar to the maritime *R. siliquosa* complex in the northern hemisphere as it is made up of taxa which produce six different acids; four of the acids are depsides and two are depsidones (viz. sekikaic acid, divaricatic acid, cryptochlorophaeic acid, boninic acid, norstictic, and salazinic acids), but these acids are not closely related biosequentially (Elix, in litt.).

Morphologically only the salazinic acid taxon is distinguishable; the other taxa show only slight morphological variations from one another, none of which is sufficiently unique and consistent that the chemical constituents of every individual can be infallibly predicted from appearance alone.

Culberson, Culberson & Johnson (1977) found a correlation between the chemistry in the *R. siliquosa* taxa and different amplitudes of ecological tolerance of each taxon. Accordingly, a study of the thalli belonging to the *R. subfraxinea* complex was undertaken in order to find if a particular chemotype could be related to a particular type of habitat based on the amount of exposure to the sea (e.g. exposed = on trees or rocks facing the open sea; sheltered = on trees growing on the landward fringe of a mangrove community or on trees in clay pan habitats).

In Table 3 the type of habitat (exposed or sheltered) at each location site is compared with the percentage of thalli containing each acid found at the site. The table shows that there is a difference in the percentage of certain acids at each site. The cryptochlorophaeic acid taxon occurs in areas experiencing the greatest amount of exposure to the open sea, the boninic acid taxon is generally found in exposed habitats (usually adjacent to quiet water), whereas the thalli containing sekikaic acid, divaricatic acid, or norstictic acid are mainly found in sheltered well protected areas away from salt spray. Salazinic acid containing thalli appear to tolerate a broad spectrum of habitats from exposed to sheltered.

From Table 3 it can be seen that there is a definite tendency for different chemotypes to occupy some microhabitats more commonly than others.

This environmental selection of different chemotypes into separate habitats is also apparent to a larger extent along the more tropical coastline of Australia (e.g. north of latitude 16°30′S), where collections made from any one site always contain only one chemotype. When the type of habitat was considered it was found that collections from Princess Charlotte Bay (a vast area of clay pan) contained sekikaic acid, whereas thalli collected from the exposed shorelines of the small tropical islands of Ingram I., Turtle I., and Sue I. all contained cryptochlorophaeic acid; thalli collected from Lizard I. all contained salazinic acid.

Although the collections from these northern regions may not have been as numerous as those to the south, enough material was collected at each site to make these findings plausible.

Table 3 Medullary metabolites expressed as a percentage of total number of specimens collected at various sites in relation to type of habitat and latitude.

Latitude °S	Location	Type of habitat	Boninic	Cryptochlorophaeic	Sekikaic	Norstictic	Salazinic	Divaricatic	Number of thalli collected
16	Daintree River	sheltered	—	—	23	—	37	40	87
16	Mossman	sheltered	—	29	63	—	8	—	38
17	Mission Beach	exposed	—	75	10	—	15	—	20
18	Murray River	exposed	—	40	—	33	27	—	15
18	Hinchbrook I.	sheltered	1	42	24	15	16	2	82
19	Townsville	exposed	—	59	29	12	—	—	17
20	Bowen	exposed	3	94	—	3	—	—	33
21	Hallidays Bay A.	sheltered	—	—	32	68	—	—	34
21	Hallidays Bay B.	exposed	—	94	—	6	—	—	35
21	Eimeo	sheltered	25	35	4	36	—	—	28
22	St Lawrence	sheltered	9	8	14	69	—	—	70
23	Keppel Sands	exposed	—	96	—	4	—	—	46
23	Gladstone	sheltered	3	42	30	25	—	—	60
24	Turkey	sheltered	4	48	48	—	—	—	33
25	Burnett Hds	exposed	10	90	—	—	—	—	23
26	Hervey Bay	exposed	36	64	—	—	—	—	22
27 28	Moreton Bay	exposed	1	99	—	—	—	—	100
29	Clarence R.	exposed	66	34	—	—	—	—	23

Distribution patterns in relation to climatic indices

The distinct distribution patterns of the Ramalinae indicate that there are differences in the ecological requirements of each taxon. The composite map of the distribution of all of the taxa (Fig. 1) shows that geographically the distributions lie in either the tropical or the temperate zones with some taxa overlapping in the intermediate zones (e.g. subtropical and warm temperate). In the higher plants it has been recognized that plants growing under tropical conditions have different growth responses compared to plants growing under temperate conditions, and that such responses are closely related to thermal optima for photosynthesis (Specht, 1981*c*; Nix, 1982).

As a knowledge of the major climatic indices which regulate plant response (e.g. temperature, precipitation, and solar radiation) has proved valuable in understanding the distribution of the phanerogram flora of Australia, it seemed reasonable to examine their value in understanding the distribution of the *Ramalina* taxa throughout Australia.

Nix (1982) proposed that Australian plants can be classified in terms of their photosynthetic response to temperature. His three major groups are relevant to the pattern of Ramalinae distribution. (1) *Megatherm Group* – plants with photosynthetic optimum 26–28°C; lower threshold 10°C, upper threshold 38°C. (2) *Mesotherm Group* – plants with photosynthetic optimum 19–22°C; lower threshold 5°C, upper threshold 33°C. (3) *Microtherm Groups* – plants with photosynthetic optimum 10–14°C; lower threshold 0°C, upper threshold 25°C. These three major groupings have geographical equivalents as shown in Table 4.

Nix (1982) integrated the climatic factors, temperature, precipitation, and solar radiation into a single multifactor Growth Index (G.I.). The Growth Index is different for plants with different thermal growth responses. Figs 4A–B and 5A indicate the distribution of megatherm, mesotherm, and microtherm plants respectively with G.I. values >0·45 and G.I. values >0·30

Table 4 Thermal divisions of Australian plant biota and their geographical equivalents, as suggested by Nix (1982).

Thermal divisions	Mean annual temperature	Geographical equivalent
Megatherm	24°C	tropical
Megatherm/Mesotherm interzone	20–24°C	subtropical
Mesotherm	14–20°C	
Mesotherm/Microtherm interzone	12–14°C	warm temperate
Microtherm	<12°C	cool temperate

<0·45 in the first two groups and with G.I. values <0·6 to >0·2 in the latter. The multifactor Growth Index (G.I.) has values ranging from zero to unity and can never exceed the value of the single most limiting factor. It is apparent from Fig. 4C, that *Ramalina* taxa occur only in those areas with a G.I. larger than 0·30 in at least one thermal response category.

The distribution pattern of each *Ramalina* taxon conforms in a general sense to the patterns of G.I. for megathermic, mesothermic, and microthermic phanerogams, indicating that the climatic indices which determine distribution limits for the higher plant species also create similar limits for the species of *Ramalina*.

Biogeographical division of the Australian Ramalinae

By superimposing the phanerogam thermal growth response patterns onto the distribution pattern of each *Ramalina* taxon, the latter are able to be divided into megatherm, mesotherm, and microtherm groups quite satisfactorily (Figs 4C, 5B).

(1) *The megatherm element*

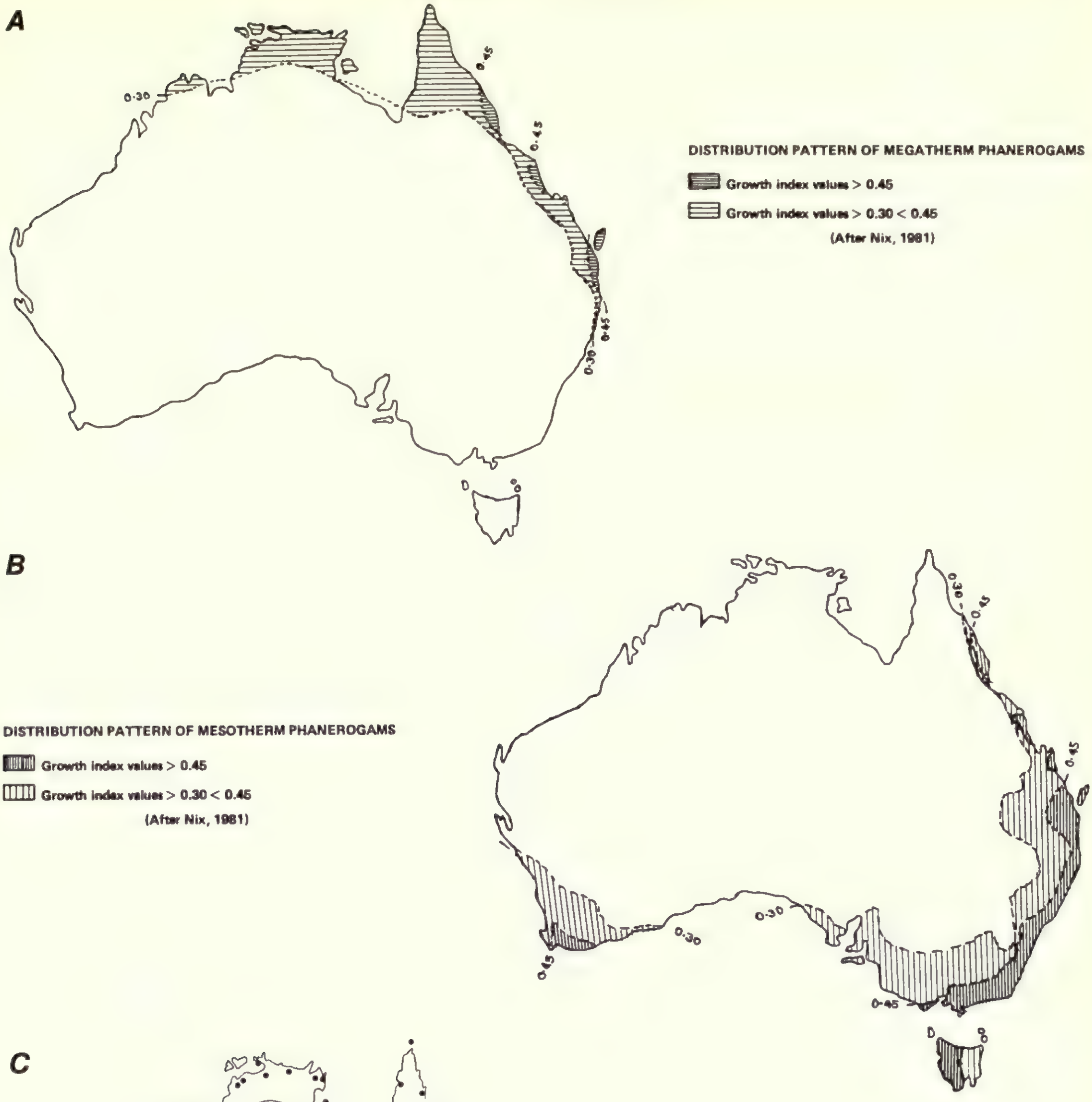
Nine of the Ramalinae can be regarded as confined to a region with a megatherm Growth Index value >0·30 <0·45. Their southern limits rarely extend below the tropics (latitudes 23°S–24°S). These taxa are *R. tropica, R. tenella, R. subfraxinea* var. *subfraxinea, R. subfraxinea* var. *norstictica, R. nervulosa* var. *nervulosa, R. nervulosa* var. *luciae,* and *R. litorea. Ramalina subfraxinea* var. *confirmata* and *R. subfraxinea* var. *leiodea* are exceptions as their southern limit reaches latitudes 33°S and 29°S respectively (Table 5). The occurrence of *R. subfraxinea* var. *confirmata* on Sue Island (latitude 9°20′S) confirms its placement in the megatherm group; *R. subfraxinea* var. *leiodea* extends to 18°S (Figs 4A, 28).

(2) *The mesotherm element*

Other *Ramalina* taxa which have an extended range along the eastern coastline are regarded as mesotherm elements as they have a southern distribution reaching the warm temperate region of Australia. These taxa are *R. exiguella, R. inflata* subsp. *perpusilla, R. peruviana*, and *R. pacifica* (Table 5). Although *R. pacifica* extends into the tropics to latitude 17°S it has been regarded as a mesotherm element because of its world distribution pattern which indicates its overall range is in the subtropics (Stevens, 1983*b*).

The presence of *R. exiguella, R. peruviana,* and *R. inflata* subsp. *perpusilla* in the tropical regions at higher elevations than sea-level is similar to the occurrence of subtropical or even temperate phanerogams which are reported to find an optimal thermal environment with increase in elevation at low latitudes (Nix, 1982). Two taxa which have restricted distribution in the mountains at altitudes exceeding 900 m are *R. filicaulis* and *R. nervulosa* var. *dumeticola.* Being rare in occurrence it is difficult to establish in what thermal group they belong. They have been tentatively placed as mesothermic plants as the former occurs in areas where *R. celastri* subsp. *celastri, R. peruviana,* and *R. inflata* subsp. *perpusilla* (all mesothermic plants) grow; and the latter must be a mesothermic offshoot of the otherwise megathermic *R. nervulosa* group.

The distribution pattern of *R. inflata* subsp. *perpusilla* covers a region corresponding to


A
0·30
0·45
0·45
0·45
0·30
DISTRIBUTION PATTERN OF MEGATHERM PHANEROGAMS
▤ Growth index values > 0.45
▤ Growth index values > 0.30 < 0.45
(After Nix, 1981)
B
0·30
0·45
0·45
0·30
0·30
0·45
0·45
DISTRIBUTION PATTERN OF MESOTHERM PHANEROGAMS
▥ Growth index values > 0.45
▥ Growth index values > 0.30 < 0.45
(After Nix, 1981)

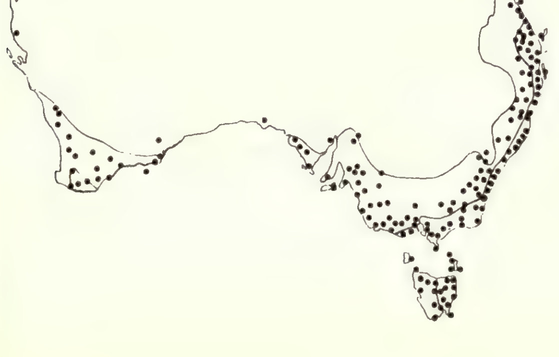


Fig. 4 A. Distribution patterns of megatherm phanerogams with G.I. values >0·30; B. Distribution patterns of mesotherm phanerogams with G.I. values >0·30; C. *Ramalina* distribution pattern with megatherm and mesotherm plant boundaries for plants with G.I. values >0·30, superimposed.

Table 5 Latitudinal distribution of the Australian *Ramalina* taxa.

Latitude °S	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
R. tropica	X		X		X	X	X																										
R. tenella					X	X	X			X	X	X	X																				
R. subfraxinea var. *subfraxinea*	X		X	X	X	X	X	X	X	X	X	X	X																				
R. subfraxinea var. *norstictica*	X	X	X	X	X		X	X	X	X	X	X	X																				
R. nervulosa var. *nervulosa*			X	X	X	X				X	X	X	X				X																
R. subfraxinea var. *confirmata*			X		X	X	X	X	X	X	X	X	X	X	X	X	X	X		X		X											
R. litorea			X						X	X		X	X																				
R. nervulosa var. *luciae*						X	X			X	X	X	X			X																	
R. exiguella			X				X			X		X	X	X	X	X	X	X	X	X	X	X	X	X									
R. inflata subsp. *perpusilla*						X	X		X	X	X	X	X	X	X	X	X	X	X		X												
R. peruviana						X	X				X	X	X		X	X	X		X	X	X	X		X	X								
R. pacifica						X	X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	X									
R. subfraxinea var. *leiodea*									X	X	X	X	X	X	X	X	X	X															
R. filicaulis												X			X		X																
R. celastri subsp. *celastri*													X		X	X	X	X	X	X	X	X	X	X	X	X	X		X	X			
R. australiensis														X				X	X	X		X	X	X		X							
R. nervulosa var. *dumeticola*															X		X	X	X														
R. inflata subsp. *inflata*																			X		X	X	X	X	X	X	X	X	X	X	X	X	
R. glaucescens																			X	X		X	X	X	X	X	X	X		X	X	X	
R. reducta																		X	X	X													
R. inflata subsp. *australis*																			X		X	X	X	X	X	X	X	X	X	X	X	X	
R. fissa																						X	X	X	X	X	X	X	X	X	X	X	
R. canariensis																						X	X	X	X		X	X	X				
R. celastri subsp. *ovalis*																						X	X	X	X	X	X	X	X	X	X	X	
R. fimbriata																								X	X	X	X			X	X		
R. unilateralis																								X	X	X	X			X	X	X	
R. whinrayi																												X	X				
R. caespitella																												X	X	X		X	

mesotherm response patterns with G. I. values above 0·30. The inland areas with G.I. values >0·30 <0·45, correspond to areas where the sekikaic acid race as well as the divaricatic acid race occur. Along the coast, the areas with G.I. >0·45 mainly produce thalli with divaricatic acid ± a trace of sekikaic acid.

To the south, the mesotherm region with G.I. values >0·45 coincides with the *R. inflata* subsp. *inflata* distribution (divaricatic acid alone or rarely + trace sekikaic acid). No specimens of the *R. inflata* complex occur in the region delimited by the mesotherm elements with G.I. >0·30 <0.45 in inland New South Wales. In the temperate southern and south-western regions of Australia *R. inflata* subsp. *australis* occupies this mesotherm region (G.I. >0·30 <0·45) and again the sekikaic acid race is present at inland sites, as well as the divaricatic acid race. Along the coastline only the divaricatic acid race is present which is a similar situation to that found with the taxon *R. inflata* subsp. *perpusilla*. Thus in the *R. inflata* complex, only taxa containing divaricatic acid ± trace sekikaic acid are found along the eastern and southern coastlines.

In the south-west corner of Western Australia both divaricatic acid and sekikaic acid taxa occur, reflecting the general aridity of this part of Australia even close to the coast.

There is a continuation of both mesotherm elements into Tasmania (Fig. 4B) and both *R. inflata* subsp. *inflata* and *R. inflata* subsp. *australis* occur, but in different regions. The *R. inflata* subsp. *inflata* taxa occur in the inland montane region whereas *R. inflata* subsp. *australis* taxa are found in the drier eastern areas (Figs 21, 22). Sekikaic acid taxa do not occur in Tasmania (extreme dryness is not a feature of the island). A microtherm influence could be responsible for the distribution pattern of the *R. inflata* subspecies in Tasmania and in many instances the presence of intermediate morphs causes difficulty in delimiting Tasmanian taxa.

Another taxon placed in the mesothermic group is *R. celastri* subsp. *celastri*. The majority of collection sites for this taxon lie within the belt with G.I. values >0·45, with a few collection localities to the west in the area covered by the mesotherm belt with G.I. >0·30 <0·45. Specimens from the latter area are always broader than coastal specimens. This taxon extends south to latitude 38°S with lessening frequency. At approximately 38°S, 145°E the mesotherm region of plants with G.I. >0·45 is replaced by the region of plants with G.I. >0·30 <0·45 (Fig. 4B). This latter region is occupied by *R. celastri* subsp. *ovalis*, a taxon which extends to Western Australia (Fig. 20). It is also found in northern Tasmania.

Ramalina australiensis occurs coastally in the mesotherm pattern with G.I. value >0·45 (e.g. Toogoom in Queensland and Yamba to Twofold Bay in New South Wales, latitudes 25°S and 29°–37°S respectively).

The main distribution of *R. canariensis* is along the southern coastline of Australia in the region with mesotherm G.I. values >0·30 <0·45 which corresponds to a Mediterranean climate region. Such environments are found in South Africa, Chile, and the Mediterranean (Raven, 1973) – all areas where this taxon occurs. The presence of *R. canariensis* at several sites along the south-east coastline of Australia may be due to suitable microhabitat conditions.

The two species found on the Bass Strait islands (viz. *R. whinrayi* and *R. caespitella*) cannot be ascribed accurately to any of the three response groups.

(3) *The microtherm element*

There are four taxa which occur in the mountainous areas of eastern and/or southeastern Australia at altitudes exceeding 600 m which can be regarded as belonging to the microtherm response group: (1) *R. reducta*, (2) *R. glaucescens*, (3) *R. unilateralis*, and (4) *R. fimbriata*.

(1) *Ramalina reducta* occurs at elevations over 1000 m in open-forests on the New England tableland. The area experiences very low winter temperatures with snow. Figs 5A–B show that it covers a region with G.I. values >0·2 <0·6.

(2) *Ramalina glaucescens* is classed as a microtherm element with its two chemical races occupying two different response groups (i) G.I. >0·4 <0·6 and (ii) G.I. >0·2 <0·4 the former region being occupied by the sekikaic acid race and the latter by the acid-deficient race (Figs 5B, 13).

(3) *Ramalina unilateralis* occurs inland and along the coast at several sites, but its distribution

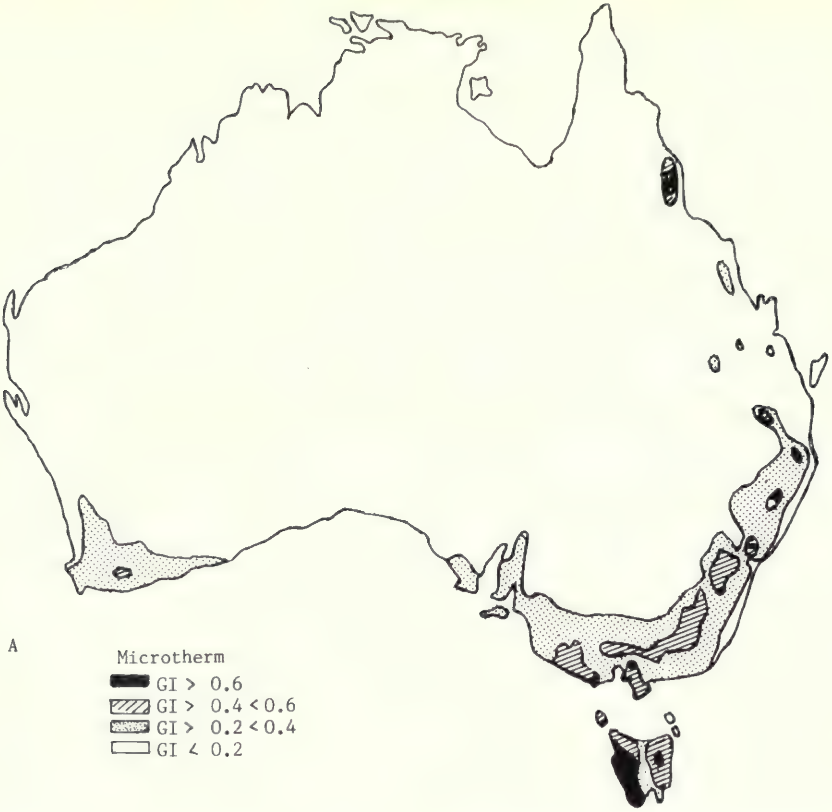


Fig. 5 A. Distribution patterns of microtherm phanerogams with G.I. values >0·2 (after Nix, 1981).

pattern corresponds with the microtherm element rather than the mesotherm element. Its range covers a region where microthermic G.I. values are >0·2 <0·6 (Fig. 5B).

(4) *Ramalina fimbriata* grows on rock outcrops at high altitudes in the open-forest country of temperate southeast Australia (Fig. 5B); its range covers a region where microthermic G.I. values are >0·2 <0·6.

Biogeography

Taxa in the genus *Ramalina* found in Europe and North America are generally distinct from the taxa which occur in Africa, South America, Australasia, and the Pacific Islands.

The records of *Ramalina* taxa which occur in the various regions of the world are scattered through the literature. Only the few present day revisions of the genus can be relied on to contain correct identification of the species; many publications record names of doubtful application. Those regions covered in recent reliable publications are: Canary Islands (Krog & Østhagen, 1980), East Africa (Krog & Swinscow, 1974, 1975, 1976), Fennoscandia and the British Isles (Krog & James, 1977), Europe (Poelt, 1969), and the West Indies (Landrón, 1972).

Although the Ramalinae of North America have not been completely revised, many of the taxa have been recently investigated by Hale (1978), Rundel (1978*a*), Bowler (1977), Bowler & Rundel (1972*a*, 1972*b*, 1973, 1974, 1978), Rundel & Bowler (1974, 1976), Hale & Culberson (1970), and Moore (1968). Less recent studies cover the Hawaiian lichens (Magnusson & Zahlbruckner, 1945; Magnusson, 1956); the Chinese Ramalinae (Zahlbruckner, 1930) and the Japanese Ramalinae (Asahina, 1938, 1939).

The South American Ramalinae are in need of revision but records of taxa collected in various regions of that continent appear in publications of Vainio (1890), Malme (1934), Follmann

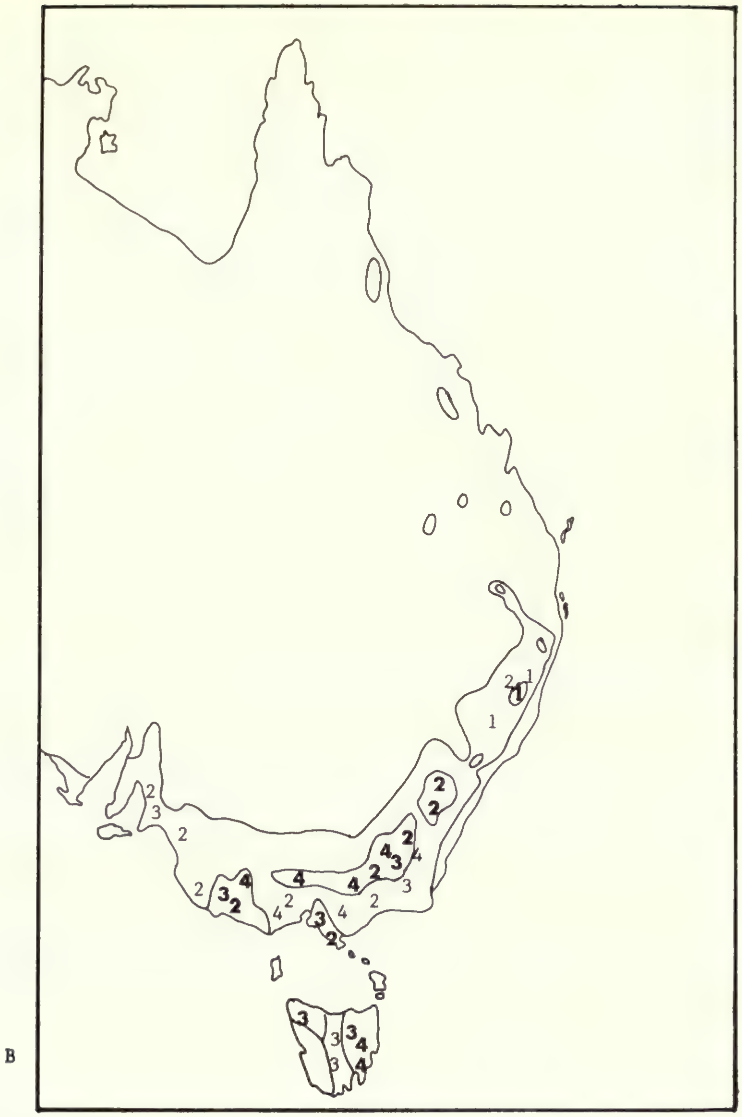


Fig. 5 B. Four *Ramalina* taxa with distribution patterns within the microtherm boundaries: 1 = *R. reducta*, 2 = *R. glaucescens* (sekikaic acid race), 3 = *R. unilateralis*, 4 = *R. fimbriata*.

(1967), Rundel (1978*b*), Osorio (1970*a*, 1970*b*, 1972, 1978), and Osorio, Aquila & Zanette (1980), as well as others. Papers with *Ramalina* taxa found on the Pacific Islands are listed in Appendix A of *Lichen Ecology* (Hawksworth, 1977). The 'Catalogue of lichens from India, Nepal, Pakistan and Ceylon' (Awasthi, 1965) was consulted to obtain species numbers in India, as no information concerning the present revision of Indian Ramalinae was obtainable from India. Nine *Ramalina* taxa are described for New Zealand (Galloway, 1985).

From the above mentioned records and personal knowledge, some idea of the global distribution of the taxa which occur in Australia was obtained (Table 6, Fig. 6). Table 6 shows that Africa has the greatest number of species in common with Australia (50%). This close relationship with African lichens was mentioned by Rogers & Stevens (1981). New Zealand and South America have the next highest percentages of species in common with Australia. It is

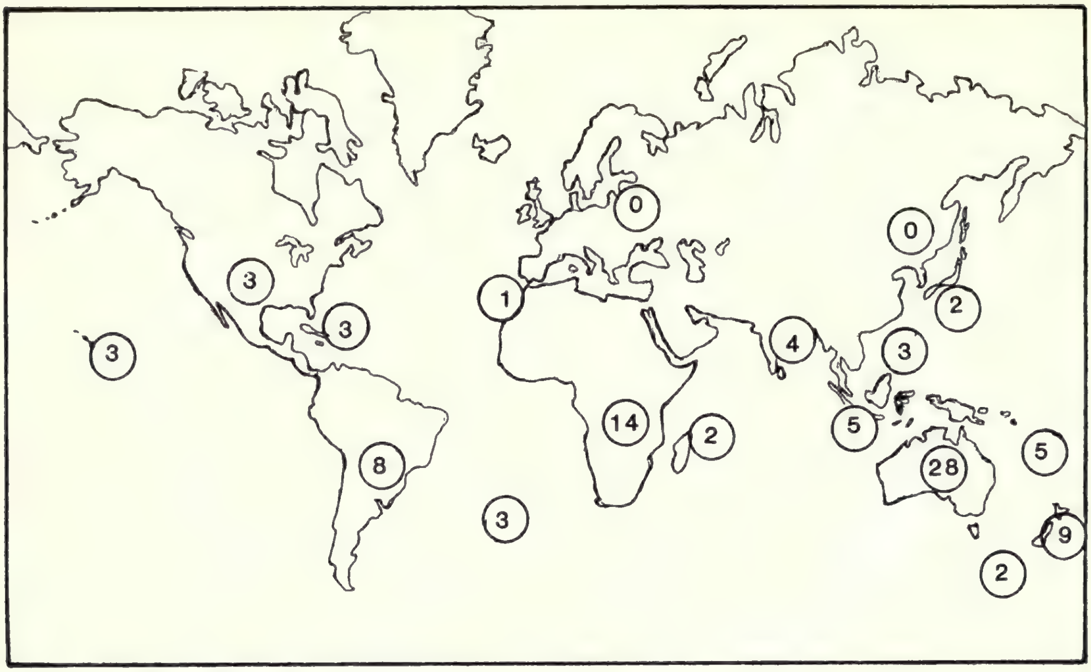


Fig. 6 Global distribution of *Ramalina* species found in Australia.

interesting that (as far as could be ascertained) there is little similarity of species between India and Australia (see below). The lack of correlation between Australian taxa and those of North America, Europe, and Asia, confirms that the greatest similarities are found in countries which have a former Gondwanaland origin.

Palaeobiogeography

Before presenting an interpretation of the likely palaeobiogeography of the Ramalinae, an understanding of some aspects of the Earth's geological history has to be appreciated.

(1) *Geological history of Gondwanaland*

The geological events that took place during the Cretaceous and Tertiary Periods which are so vital to the understanding of the distribution patterns of plants are summarised in Table 7.

The early ideas of land bridges between continents and the later theory of Continental Drift have been superseded by the theory of Plate Tectonics. This theory is now generally accepted by most geologists to account for the separation of continents which show evidence of having been once grouped together as a Pangaea or super-continent, or as two large continents, Laurasia (north) and Gondwanaland (south). In this theory, the continents break up by rifting and separate by sea-floor spreading. New oceanic crust is formed at spreading ridges and consumed in subduction zones. The theory of an expanding earth (Carey, 1976) obviates the necessity for subduction zones and produces a more neatly-fitting Pangaea than other models, especially in the closer fit of northern and north-west Australia with Asia, making the distribution of now distant but similar biota more easily understood; unfortunately this theory has not had general acceptance.

(2) *Plant distribution related to geological events*

The map of the Gondwanaland continent during the Cretaceous Period (130–100 m.y. B.P.) [Fig. 7] shows the relevant palaeolatitudes at that time (Powell, Johnson & Veevers, 1981). Raven & Axelrod (1974) stated that direct migration from South America and Africa via

Table 6 The global distribution of the *Ramalina* taxa occurring in Australia.

Ramalina species	Australia	Africa	South America	New Zealand	India/Sri Lanka	Islands of the Pacific Ocean	Islands of the Indian Ocean	Tristan da Cunha	Europe	North America	West Indies	China
R. australiensis	*			*								
R. caespitella	*											
R. canariensis	*	*	*						*			
R. exiguella	*	*		*								
R. filicaulis	*											
R. fimbriata	*	*		*								
R. glaucescens	*			*								
R. litorea	*						*					
R. peruviana	*	*	*	*	*	*		*		*	*	
R. reducta	*	*										
R. tenella	*	*	*			*						
R. unilateralis	*	*	*									
R. whinrayi	*											
R. celastri												
subsp. *celastri*	*	*	*	*	*	*		*		*	*	
subsp. *ovalis*	*	*	*	*				*				
R. inflata												
subsp. *inflata*	*	*	*	*		*				*	*	*
subsp. *perpusilla*	*											
subsp. *australis*	*											
R. fissa	*											
R. nervulosa												
var. *nervulosa*	*	*					*					
var. *luciae*	*	*			*	*						
var. *dumeticola*	*	*			*	*						
R. pacifica	*	*		*		*						
R. subfraxinea												
var. *subfraxinea*	*		*									
var. *leiodea*	*					*						
var. *confirmata*	*					*	*					
var. *norstictica*	*											
R. tropica	*											
TOTALS	28	14	8	9	4	9	3	3	1	3	3	1

Antarctica to Australia was possible at this time (Table 7). Even in the late Cretaceous, Australia still had connections with South America through Antarctica, but the migration of plants via the southern route probably became progressively reduced until finally stopped by the break of Australia from Antarctica in the Eocene (53–38 m.y. B.P.). The early break-away of India from the rest of Gondwanaland (125–100 m.y. B.P.), and its rafting north across the equator with the loss of some Gondwanaland species, could account for the lack of taxa similar to the Australian Ramalinae.

Two major pathways of dispersal of the higher plants from west Gondwanaland have been postulated by plant biogeographers: (1) a temperate migration route via Antarctica from west Gondwanaland (i.e. South America and Africa), to Australia and New Zealand, and (2) a tropical route from East Africa to Madagascar, the islands of the Indian Ocean and Indo-Malaysia to Australia (Croizat, 1952; Raven & Axelrod, 1974). As the *Ramalina* species found in Australia can be placed in a range of temperature response groups from cool temperate to

Table 7 The history of the break-up of Gondwanaland, indicating available migration routes (from Raven & Axelrod, 1974 and Powell, Johnson & Veevers, 1981).

Million years BP	Geological periods	Event/geographic situation
125	early Cretaceous	Africa and South America begin to split; India begins to split from Australia/Antarctica but remains attached to Madagascar.
110 + 10		Direct migration between west Gondwanaland and Australia ceases.
100	mid Cretaceous	Direct migration between Africa and Madagascar still possible. India rafts northwards and is completely separated from Australia and Antarctica; no exchange of species possible. Migration of species between Africa and Australia via east Antarctica still possible.
90		Africa and NE. Brazil separated by a narrow strait; migration possible at this point. Africa and South America separated by 800 km of ocean but numerous islands linked them along the mid-Atlantic Ridge. Australia ceases to have any migration from Africa.
80	late Cretaceous	Australia/Antarctica extend from 40°S to the polar region. South America closely connected with Antarctica 80–30 million years BP. Separation of New Zealand and New Caledonia from Australia.
63	early Palaeocene	Africa and Europe connected at Spain and possibly with Asia at Arabia, allowing both northward and southward migration.
55	Palaeocene-Eocene	Oceanic crusts form between Antarctica and Australia; northern edge of Australia now at 30°S and commencement of separation of Australia from Antarctica.
49	mid Eocene	Separation of the continental margins of Australia and Antarctica but another 10 m.y. of migration of species from South America through Antarctica to Tasmania along the South Tasman Rise before final separation.
45		Direct migration between India and Asia.
30	mid Oligocene	The leading edge of Australia as it rafts northwards still south of the latitude of the Sunda Arcs.
20	early Miocene	Initial contact between Sunda Arc and New Guinea (abundant precipitation).
10	late Miocene	Collision of Australia with the Sunda Arcs. Antarctic ice-sheet rapid expansion (lowered precipitation).
Present	Holocene	Australia moves towards the equator at 66 mm year^{-1}.

tropical, it could be hypothesised that their routes of entry to Australia were from both the south (the microtherm and mesotherm taxa) and from the north (the megatherm taxa).

(3) *Dispersal and migration*

Any postulates concerning the migration pattern of the Ramalinae from a centre of origin are purely hypothetical as no fossil records are available and any assumptions made are based on the migration pathways of the higher plants deduced from fossil records. The approach used in this study is similar to that of Jørgensen (1983) and Sipman (1983) although the writer does not agree with all of their conclusions.

Biogeographic evidence suggests that many genera and families of gymnosperms and angiosperms had evolved before the breakup of Gondwanaland began in the Cretaceous, and had arrived in Australia from South America and Africa via Antarctica during the middle

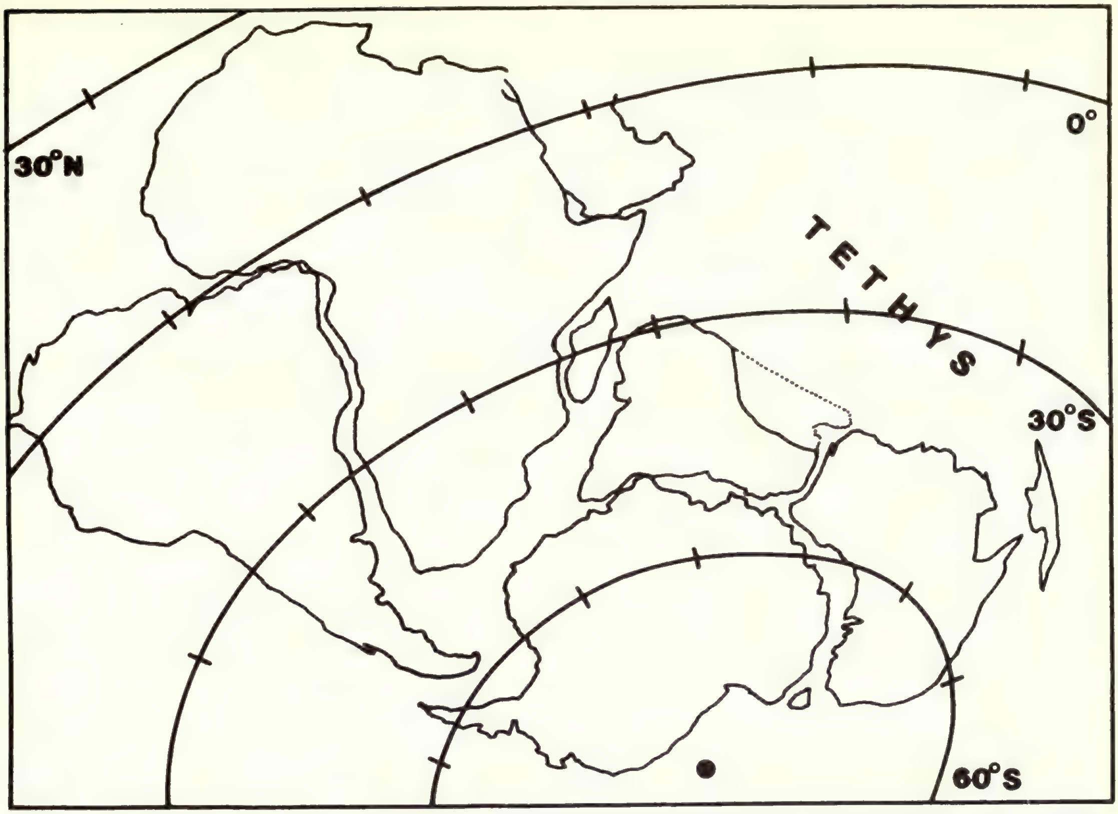


Fig. 7 Position of east and west Gondwanaland in the early to mid-Cretaceous (130–100 m.y. B.P.). Ticks show longitudes which have no fixed origin (Adapted from Powell, Johnson & Veevers, 1981).

Cretaceous (108–100 m.y. B.P.). Fossil evidence indicates that many of the Gondwanan families and genera had occupied Australia by the early Tertiary (63–55 m.y. B.P.) (Specht, 1981*c*).

(a) *Step by step dispersal:* Schuster (1979) stated that migration of land plants normally tends to be by short range dissemination as members of structured communities, and he proposed that the dispersal of Hepaticae occurred as part of the dispersal of whole plant communities. It is also reasonable to hypothesise that the *Ramalina* species also made this step by step spread across the continents of Laurasia and Gondwanaland with the migrating structural communities during the Cretaceous-early Tertiary.

This suggested step by step migration of plant communities appears to be a valid means of dispersal as this enables plants which have similar habitat requirements to expand as a whole, in favourable climates, and so migrate when conditions are favourable and disappear from areas where environmental conditions have deteriorated. It seems highly likely that under the circumstances lichens which grow within these communities would migrate at the same rate and in the same direction.

If step by step migration halted with sea-floor spreading of the continents, then another means of dispersal has to be proposed. Seeds of the higher plants have been found to be carried by birds and animals over long distances; the lighter seeds being wind dispersed. The Ramalinae produce both spores and vegetative diaspores and it is feasible that these could be wind dispersed or carried by birds.

(b) *Wind dispersal:* If long distance dispersal of spores by the wind is accepted then this means of dispersion would have been in operation in early times. It is reported by Raven & Axelrod (1974) that with the separation of Australia and Antarctica in the Eocene, there was a strengthening of the circum-Antarctic wind which could have carried spores from South America to Australia, Tasmania, and New Zealand.

The success of a spore in a new environment would need the availability of a suitable phycobiont and the lack of competition from plants already in the area. With the vegetative diaspore both partners arrive together so that provided the environment is hospitable to their genetic requirements they will readily become established in the new habitat. Spores can become established after long distance wind dispersal since fertile lichen species have been found on the islands of Hawaii. Jørgensen (1979, 1983) remarked on the efficiency of wind dispersal of lichen spores in the population of the remote island of Tristan da Cunha.

If the original dispersal of the Ramalinae is comparable with the original dispersal of angiosperms and gymnosperms, then their migration from west Gondwanaland may have taken place by both step by step migration and wind dispersal, with the latter means continuing after the break up of the continents.

(4) *Centres of origin*

The centre of origin of a group is often regarded as that area having the greatest concentration of species. Hale used this method in assessing the centre of origin of the genera *Relicina* (Hale, 1975), *Pseudoparmelia* (Hale, 1976*a*), *Parmelina* (Hale, 1976*b*), and *Bulbothrix* (Hale, 1976*c*).

If the numbers of *Ramalina* taxa occurring in each landmass that once formed Gondwanaland are estimated (and these numbers must be only approximate as without recent revisions many names could be synonyms or misidentifications) then it is found that 41 Ramalinae occur in South America, 42 in Africa, 36 in India, and 30 in Australasia.

South America and Africa (once West Gondwanaland) appear to have the largest number of Ramalinae and could be regarded as the centre of origin of the southern hemisphere taxa.

The occurrence of high numbers of taxa within the one genus, in a particular region, can, however be due to a re-radiation of species after the original dispersal of the taxa. When an environment is free of competitive species, newly evolved taxa belonging to the genus will become established. This situation has been found in Western Australia amongst the eucalypts, where secondary radiation of species has occurred in a region where there is little competition from other genera (Pryor, 1981).

Such a situation may have arisen in Australia with the evolution of the mangrove flora in this region (Specht, 1981*b*). Mangroves are the major phorophytes for the present day *R. subfraxinea* complex. It is proposed that the ancient stock of the *R. subfraxinea* group could have entered Australia via the northern route from East Africa (as this group is regarded as a megatherm response group) and become established along the Australian tropical coastline on the newly evolved mangroves. The occurrence of all six chemotypes in the region around latitude 18°S indicates an area of speciation from where secondary radiation could have spread to the east and west.

(5) *Vicariant taxa*

The Croizat theory of vicariance biogeography (Croizat, 1952; Croizat, Nelson & Rosen, 1974) postulates that species which are ecologically similar but occur on different land masses have a common ancestry. They are regarded as disjunct populations of once continuously distributed taxa which have undergone speciation as physical disruption occurred and Croizat cited many Gondwanaland taxa to support his theory. Galloway (1979) employed the same ideas in his comments on the distribution of species in the genera *Usnea, Pseudocyphellaria, Psoroma*, and *Stereocaulon*.

A number of taxa belonging to the Fistularia group in Australia appear to be part of the vicarant taxa of Gondwanaland origin. For example the Australian taxon *R. inflata* subsp. *perpusilla* has an ecotype which grows on mangroves and closely resembles the East African species *R. consanguinea* which also occurs on mangroves with the main difference in the spore size; in some habitats in Australia *R. inflata* subsp. *inflata* morphology closely resembles some forms of the East African taxon *R. calcarata*, but their chemistry differs in the minor constituents.

Chemical difference is the only character which separates the Australian taxon *R. filicaulis* from the American taxon *R. anceps*. Material similar to the Australian material, and also lacking medullary acids, has been cited from South Africa. It is proposed that all three continents possess species which could be regarded as vicariant taxa belonging to the *R. usnea* complex, as they are ecologically and morphologically similar.

On the basis of the evidence discussed above it is postulated that Australia has been populated by species of *Ramalina* since the late Cretaceous. Since west Gondwanaland is accepted as the centre of origin for the angiosperms, based on fossil evidence, there is the possibility of these acting as phorophytes for ancestral taxa of the present day *Ramalina*, as that same region is a likely centre of origin for *Ramalina*. The step by step spread of the plant communities would have enabled the Ramalinae to spread by one of two migration routes either (1) the southern route from South America (after Africa had separated) via the Scotia arc, Antarctica to Tasmania and Australia or (2) the northern migration route from East Africa via Madagascar, the Mascarenes, Indo-Malaya to northern Australia, by which means the megathermic Ramalinae could have reached tropical Australia. Once established in Australia the megatherm *Ramalina* taxa remained a maritime group as inland habitats would have been inhospitable. Secondary radiation from Australia by some of the megathermic taxa appears to have occurred with the spread of species to the Pacific and Indian ocean islands.

The microtherm Ramalinae became established in the mountainous region of southern Australia since these habits would have suited their thermal response patterns as Australia drifted northwards and the temperatures increased.

The climatic changes that occurred in the late Miocene Period caused the desiccation of the continent. Subsequent speciation of mesotherm Ramalinae could have occurred producing taxa which occupied the new and dryer habitats of the south-west and west of Australia.

In this way the present distribution pattern of the Australian Ramalinae reflects their palaeobiogeographic and palaeoecological history.

Taxonomy

The delimitation of *Ramalina* species proved difficult owing to the amount of morphological variation shown by each taxon. A large amount of material had to be examined in order to ascertain what concepts should be applied in the delimitation of each taxon. Three taxonomic ranks have been used.

Taxonomic ranks

(1) *Species:* The rank of species has been given only to those taxa which can be recognized by several distinct morphological traits which collectively produce a particular thallus type (allowing for an appropriate amount of variation), together with a set of specific anatomical and chemical properties, and which show a distinct habitat and distribution range.

Difficulties arose when two or more chemotypes produced a single morphotype; this problem had to be resolved by considering the habitat and distribution range of the taxa, and if the only difference found was in the chemistry then these chemical races were treated as conspecific.

The concept of species pairs (Artenpaare), as proposed by Poelt (1970, 1972) is that species which reproduce by vegetative methods (secondary species) have been derived from existing or extinct fertile species (primary species), and that primary and secondary species have identical (or closely related) chemical components. This view is held by most lichenologists and species pairs have been found in many genera e.g. in the *Physcia* and allied genera (Moberg, 1977), *Parmelia* sect. *Hypotrachyna* (Culberson & Hale, 1973), *Dirina* (Tehler, 1983), and to a lesser extent in *Alectoria* (Brodo & Hawksworth, 1977).

Only a few records of species pairs have been found in the Ramalinae. Rundel & Bowler (1976) discussed *R. leptocarpha* and *R. sublectocarpha* as a fertile-sorediate species pair and Krog & Østhagen (1980) have commented that the fertile species *R. implectens* may be regarded as the parent morph of the sorediate species *R. farinacea*.

None of the Australian sorediate Ramalinae is regarded as derived from any of the fertile taxa found in Australia today.

(ii) *Subspecies:* The delimitation of a taxon based on well marked discontinuities in characters was not always possible. Some *Ramalina* taxa were found to intergrade into each other, differing only subtly morphologically yet extending over large areas. When such complexes were examined carefully the most obvious morphological changes were found to coincide with different geographical regions.

The term subspecies has therefore been applied to a taxon which could be shown to occupy a particular region within the total distribution range of a large complex (as defined by Hawksworth, 1976). This taxon can be extremely variable within its geographical confines and can produce several ecotypes which occupy separate habitats.

As subspecies intergrade into each other, their delimitation is much more arbitrary than that of a species, and depends more on geographical divisions than on chemical or morphological differences. Imshaug & Brodo (1966) pointed out that the use of the rank of subspecies permitted a classification which is not only practical but one which indicates a possible phylogenetic system. The evolutionary relationships that may exist in some of the Australian taxa have been indicated by the use of the rank of subspecies.

(iii) *Variety:* The rank of variety has been used when more or less morphologically identical taxa have been found to produce different chemistries which correlate with distinctive distribution patterns.

The production of either divaricatic acid or sekikaic acid in populations of the one taxon posed a nomenclatural problem. Several lichenologists have mentioned the same difficulty e.g. in the genus *Dirinaria* (Jørgensen, 1974) and in the genus *Ramalina* (Imshaug, 1972; Rundel, 1978*a*). The solution has been to regard both acids as representing chemical races within the one taxon.

Hybridization

It is not easy to establish the genetic homogeneity or heterogenity of lichenized fungi. Jahns (1974) pointed out that thallus or hyphal fusions do occur in lichens, which could enable a form of hybridization to take place. A specimen of *R. leiodea* recorded by Elix (1982) as being a 'schizophrenic thallus', had 'left-hand branches containing one acid, the right-hand branches another and the central branches containing a mixture of both'. In this case the two acids involved were two depsides, not closely related (cryptochlorophaeic acid and boninic acid). Another such combination of two acids in one specimen belonging to the *R. subfraxinea* complex has been found during the present study; the specimen was collected at Hinchinbrook I. where all acid races of the *R. subfraxinea* complex are present. The thallus concerned contained both boninic acid and salazinic acid, one a depside and the other a depsidone. As these two acids are not biosequential metabolites it appears likely that this is a similar form of hybridization to that found by Elix (1982), and that both could be regarded as 'chimeras' produced by the fusion of hyphae from two different spore types. It is not known what chemistry the thalli produced from spores of this plant would have. No other thalli with this combination of acids has been found.

The occurrence of sekikaic acid in the divaricatic acid race of *R. subfraxinea* var. *subfraxinea* is regarded as different from the above. Sekikaic acid and divaricatic acid are reasonably closely related biosequentially and apparently can interconvert (Elix in litt.) which would result in chemical combinants if the conversion was incomplete. However the hypothesis of interspecific hybridization (Brodo, 1978) remains feasible and has to be considered beside the hypothesis that incomplete conversion of a precursor acid occurs during the biosynthetic steps from one acid to another (Bowler & Rundel, 1978). If hybridization is accepted as the cause of this mixture of acids then it would be natural to expect the proportions of each acid to be equal in the thallus. However, this was not the case with the taxa examined; in all instances divaricatic acid occurred in far larger quantities than did the sekikaic acid. It is therefore suggested that incomplete conversion of one acid to another has taken place.

Table 8 Taxonomically important characters in the Australian *Ramalina* taxa.

						major acid constituents								
						orcinol depsides					β-orcinol depsidones			
	substrate		thallus			*para-*		*meta-*						
Ramalina species	corticolous	saxicolous	solid	inflated	sorediate	divaricatic	evernic	sekikaic	cryptochlorophaeic	boninic	salazinic	norstictic	psoromic	nil acids
R. australiensis	X	X	X											X
R. caespitella		X	X		X			X						
R. canariensis	X		X		X	X								
R. exiguella	X		X											X
R. filicaulis	X		X											X
R. fimbriata		X		X	X	X								
R. glaucescens	X		X			X		X						
R. litorea		X	X				X							
R. peruviana	X		X		X			X						
R. reducta	X		X		X								X	
R. tenella	X		X		X						X			
R. unilateralis	X	X	X		X	X								
R. whinrayi		X	X			X		X						
Species complexes														
R. celastri														
subsp. *celastri*	X	X	X											X
subsp. *ovalis*	X		X											X
R. inflata														
subsp. *inflata*	X			X		X								
subsp. *perpusilla*	X			X		X		X						
subsp. *australis*	X	X		X		X		X						
R. fissa	X	X		X							X			
R. nervulosa														
var. *nervulosa*	X		X		X	X								
var. *luciae*	X		X		X			X						
var. *dumeticola*	X		X		X			X						
R. pacifica	X	X	X		X						X			
R. subfraxinea														
var. *subfraxinea*	X		X			X		X						
var. *leiodea*	X		X							X				
var. *confirmata*	X	X	X						X					
var. *norstictica*	X		X									X		
R. tropica	X	X	X								X			

Description of the genus *Ramalina*

Ramalina Ach., *Lichenogr. Univ.*: 122,598 (1810), nom. cons.
Thallus fruticose, greenish-grey, pale green or greenish-yellow, caespitose, erect, subpendulous to pendulous; branching dichotomous, subdichotomous to irregular or dense intricate; branches few to many, twig-like, strap-like to palmate, flat, subterete or terete, solid or inflated; apices forked, attenuate, rounded; surface shiny or matt, smooth or rugose, pseudocyphellate; holdfast delimited or dispersed; soralia small and punctiform to large and round or elongate;

cortex composed of two layers, the outer cortex hyphae more or less anticlinal or randomly oriented, the inner cortex hyphae periclinally arranged; hyphae surrounded by a large amount of matrix; medullary hyphae loosely interwoven between the upper and lower cortex or confined to the algal zone.

Apothecia terminal, subterminal, marginal, lateral, laminal; convex, plane or concave, sometimes incised; disc pale to flesh coloured; margin concolourous with thallus; asci clavate, containing 8 spores; spores hyaline, oblong, ellipsoid or fusiform, straight or curved, 1-septate. Pycnidia inconspicuous, pale, usually rare in Australian species.

The algae are Trebouxioid, globose, forming an irregular ring along the edge of the inner cortex; when confined to the upper side only the thallus becomes dichroic with a white lower surface.

Type species (conserved): *Ramalina fraxinea* (L.) Ach.

Enumeration of the Australian taxa

The Australian Ramalinae comprise 28 taxa which can be grouped into 17 fertile and 11 sorediate taxa. Sixteen species have no subspecific taxa recognized, and four species contain a total of 12 subspecific taxa.

Table 8 lists the taxonomically important attributes of each of the 28 taxa; those belonging to species complexes are placed after the alphabetically arranged single species, as is also done in the description of the taxa. The disposition of the other *Ramalina* taxa recorded by Wetmore (1963) and Weber & Wetmore (1972) is shown in Appendix 1.

The specimens examined are cited with location, latitude and longitude in degrees, type of substrate, date, the collector's name and the herbarium abbreviation (Holmgren, Keuken & Schofield, 1981). Collectors initials have been used for those collectors whose specimens are cited most frequently in this work. These names have been abbreviated as follows:

AA	*A. Archer*	*JC*	*J. Cashin*
ED	*E. Dahl*	*JW*	*J. S. Whinray*
GB	*G. C. Bratt*	*NCS*	*N. C. Stevens*
GK	*G. Kantvilas*	*NS*	*N. Sammy*
GNS	*G. N. Stevens*	*RF*	*R. B. Filson*
HS	*H. Streimann*	*RS*	*R. D. Seppelt*
JAE	*J. A. Elix*	*RWR*	*R. W. Rogers*

Only one specimen is cited from each location for most of the taxa; where the taxon grows profusely over a wide area, only specimens from selected sites are listed: viz, *R. celastri* subsp. *celastri, R. celastri* subsp. *ovalis, R. inflata* subsp. *inflata, R. inflata* subsp. *perpusilla, R. inflata* subsp. *australis*, and *R. fissa*.

Key to *Ramalina* in Australia

1a.	Thallus inflated (partially or totally)	35
1b.	Thallus not inflated	2
2a (1b).	Plant saxicolous	3
2b.	Plant corticolous	12
3a (2a).	Thallus sorediate	4
3b.	Thallus not sorediate	5
4a (3a).	Soredia eruption through eroded lower surface and at apices	**6. *R. fimbriata*** (p. 161)
4b.	Soredia contained in well defined soralia, which are marginal and sometimes laminal	**2. *R. caespitella*** (p. 155)
5a (3b).	Thallus made up of a few loose branches	6
5b.	Thallus composed of numerous branches forming a dense cushion	8
6a (5a).	Branches compressed, flat (apothecia marginal)	**14. *R. celastri*** subsp. ***celastri*** (p. 180)
6b.	Branches subterete to terete	7
7a (6b).	Branching dense, distal, K− (no medullary acids)	**1. *R. australiensis*** (p. 152)
7b.	Branching sparse, K+ red (salazinic acid)	**20. *R. tropica*** (p. 210)

8a (5b). Branches solid 9
8b. Branches inflated, often split 10

9a (8a). Apothecia terminal, large 3–10 mm diam. .... **13. *R. whinrayi*** (p. 179)
9b. Apothecia subterminal (subtending narrow pointed branchlets, apothecia 1–2 mm diam.) .... **8. *R. litorea*** (p. 169)

10a (8b). Thallus showing some inflation; splitting and tattering of branches common 11
10b. Thallus not inflated 12

11a (10a). Medulla K+ red (salazinic acid) .... **19. *R. fissa*** (p. 193)
11b. Medulla K− or K+ pink (divaricatic acid or sekikaic acid) **15. *R. inflata*** subsp. ***australis*** (p. 191)

12a (2b). Thallus sorediate 13
12b. Thallus not sorediate 21

13a (12a). Lower surface of anastomosing strands resting on the medulla .... **10. *R. reducta*** (p. 175)
13b. Lower surface not of anastomosing strands only 14

14a (13b). Branches few, usually broad at base (soft textured, soralia apical and marginal) **3. *R. canariensis*** (p. 156)
14b. Branches numerous, narrow 15

15a (14b). Branches usually cartilaginous (splitting open at intervals along their length) **12. *R. unilateralis*** (p. 177)
15b. Branches not cartilaginous, complete 16

16a (15b). Medulla K+ red (salazinic acid) 17
16b. Medulla K− or K+ pink 18

17a (16a). Soralia punctiform, mainly apical on branchlets (thallus up to 3 cm high) **11. *R. tenella*** (p. 176)
17b. Soralia ellipsoidal or round, marginal on elongate branches (thallus usually 4–8 cm long) .... **18. *R. pacifica*** (p. 201)

18a (16b). Soralia ellipsoidal or round, marginal on elongate branches 19
18b. Soralia punctiform, marginal and apical (branching dense, intricate, thallus resilient in texture) .... **9. *R. peruviana*** (p. 170)

19a (18b). Medulla K+ pink (sekikaic aggregate acids) 20
19b. Medulla K− (divaricatic acid and stenosporic acid) **17. *R. nervulosa*** var. ***nervulosa*** (p. 195)

20a (19a). Sekikaic aggregate acids ± faint ramalinolic acid **17. *R. nervulosa*** var. ***dumeticola*** (p. 197)
20b. Sekikaic aggregate acids ± faint homosekikaic acid .... **17. *R. nervulosa*** var. ***luciae*** (p. 199)

21a (12b). Medulla K+ red 22
21b. Medulla K− or K+ pink 23

22a (21a). Branches flat, sometimes canaliculate, containing norstictic acid (spores 12–16 × 4–5 μm) .... **19. *R. subfraxinea*** var. ***norstictica*** (p. 208)
22b. Branches usually subterete, never canaliculate, containing salazinic acid (spores 14–22 × 4–6 μm) .... **20. *R. tropica*** (p. 210)

23a (21b). Branches subterete to terete, containing no medullary acids 24
23b. Branches flat, with or without medullary acids 28

24a (23a). Medulla K− 25
24b. Medulla K+ pink 30

25a (24a). Apothecia lateral and subterminal with branch apex appearing as a long spur (sometimes black tipped) .... **4. *R. exiguella*** (p. 158)
25b. Apothecia never subterminal nor bearing a spur 26

26a (25b). Distal branchlets occur on otherwise unbranched primary branches **1. *R. australiensis*** (p. 152)
26b. Dense distal branchlets not present 27

27a (26b). Thallus thread-like (with dichotomous branching) .... **5. *R. filicaulis*** (p. 160)
27b. Thallus fruticose 28

28a (27b). Apothecia marginal on both edges (branches may be canaliculate, no medullary acids) **14. *R. celastri*** subsp. ***celastri*** (p. 180)

28b. Apothecia not marginal on both edges ... 29

29a (28b). Apothecia laminal, numerous, and equal in size ... **14. *R. celastri*** subsp. ***ovalis*** (p. 184)
29b. Apothecia not laminal and numerous and equal in size ... 30

30a (29b). Branches broad with apices forked or lacerated, never simple and attenuate [apothecia in axils of branches (up to 5 mm diam.) or terminal on the broad margins of the apices, or small and sparsely spread laminally] ... **7. *R. glaucescens*** (p. 163)
30b. Branches usually narrow with apices simple and attenuate or bent to form a spur below apothecium ... 31

31a (30b). Branches narrow with dichotomous branching (apothecia marginal or subterminal or in the axils of branches, small 0·5–1·5 mm diam.) ... **7. *R. glaucescens*** (p. 163)
31b. Branches narrow to broad, branching usually from the base only ... 32

32a (31b). Medulla K+ pink ... 33
32b. Medulla K− ... 34

33a (32b). Branches elongate, narrow, often tuberculate, containing sekikaic acid **19. *R. subfraxinea*** var. ***subfraxinea*** (p. 203)
33b. Branches not elongate, rarely tuberculate, containing cryptochlorophaeic acid **19. *R. subfraxinea*** var. ***confirmata*** (p. 205)

34a (32b). Thallus containing boninic acid ... **19. *R. subfraxinea*** var. ***leiodea*** (p. 207)
34b. Thallus containing divaricatic acid ... **19. *R. subfraxinea*** var. ***subfraxinea*** (p. 203)

35a (1a). Thallus sorediate ... **6. *R. fimbriata*** (p. 161)
35b. Thallus not sorediate ... 36

36a (35b). Thallus button-like, bearing apothecia (3 mm diam.) between sterile branches or totally sterile with eroded apices, medullary reaction K−, saxicolous **15. *R. inflata*** subsp. ***australis*** (p. 191)
36b. Thallus not button-like nor bearing apothecia between sterile branches ... 37

37a (36b). Branches split open and tattered ... 38
37b. Branches perforate but complete ... 39

38a (37a). Thallus grossly inflated, few or no perforations, splitting open of branches, medullary acids divaricatic or sekikaic ... **15. *R. inflata*** subsp. ***australis*** (p. 191)
38b. Thallus grossly inflated or split apart, no perforations, medullary acid salazinic **19. *R. fissa*** (p. 193)

39a (37b). Thallus semi-inflated to almost compressed, apothecia never concave **15. *R. inflata*** subsp. ***perpusilla*** (p. 188)
39b. Thallus totally inflated, apothecia concave and innate **15. *R. inflata*** subsp. ***inflata*** (p. 185)

1. *Ramalina australiensis* Nyl. Plate 7, fig. 1; Plate 13, fig. 1.

in *Bull. Soc. Linn. Normandie* II, **4**: 120 (1870). Type: Australia, West Australia, Swan River, 1846, *Verreaux* s.n. (PC! – holotype; H-NYL 37491! – isotype; usnic acid).

Ramalina myrioclada Müll. Arg. in *Flora, Jena* **66**: 20 (1883). Type: Australia, New South Wales, Twofold Bay, 1882, *White* s.n. (G! – holotype; usnic acid). Plate 13, fig. 2.

Thallus corticolous, rarely saxicolous, pale green to grey-green, erect to pendulous, 3–10 cm long, exceptionally to 20 cm; branching sparse in the basal region of the primary branches, becoming dense and irregular towards the apices where small branchlets form tufts; branch width 0·2–0·5(–1·0) mm, primary branches usually subterete and fine, or thick, compressed and coarse, branches never tortulose, often subsidiary short branchlets occur at right angles to the primary branch, apices of branchlets often hooked; surface matt, smooth or furrowed, longitudinal splitting occurs on the surface in coarser forms; pseudocyphellae often present; holdfast delimited although several branches arise from it, attachment of branches to the substrate at intervals along their length may occur; soralia absent.

Apothecia uncommon, lateral on the primary branches, usually towards the base; disc

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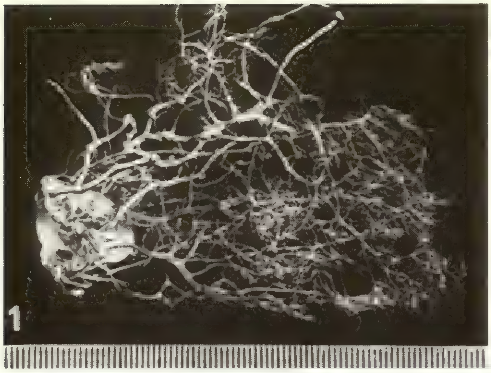
Plate 7 Thallus growth forms in the Australian Ramalinae. Scale in mm. Fig. 1 *R. australiensis*. Fig. 2 *R. caespitella*. Fig. 3 *R. canariensis*. Fig. 4 *R. canariensis* (large form). Fig. 5 *R. exiguella*. Fig. 6 *R. filicaulis*. Fig. 7 *R. fimbriata*. Fig. 8 *R. litorea*.

►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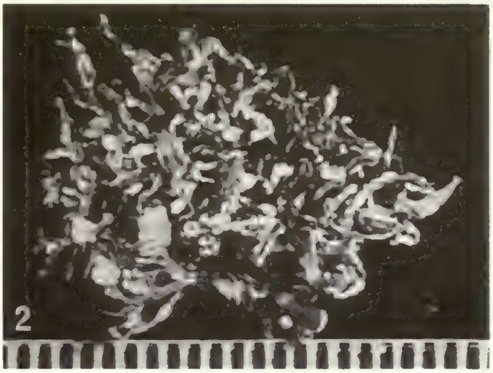
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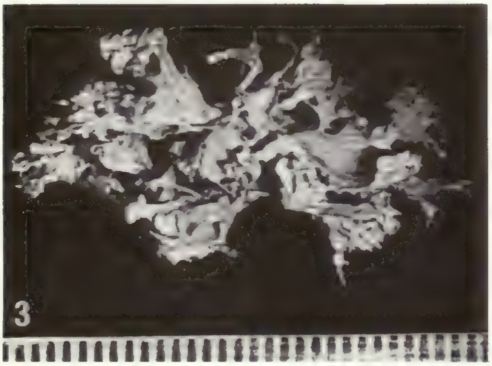
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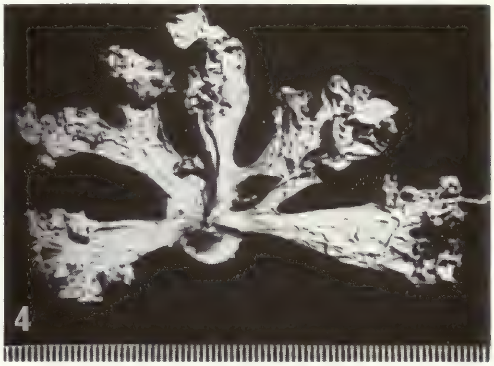
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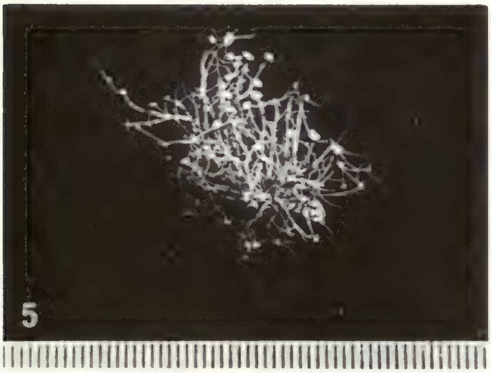
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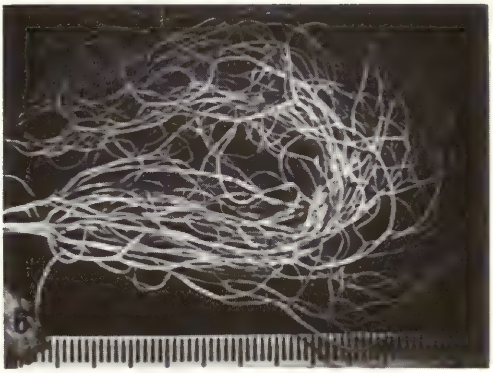
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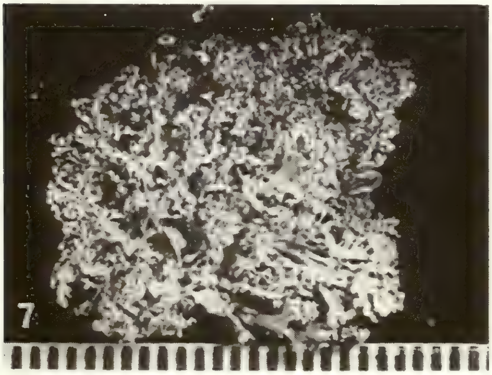
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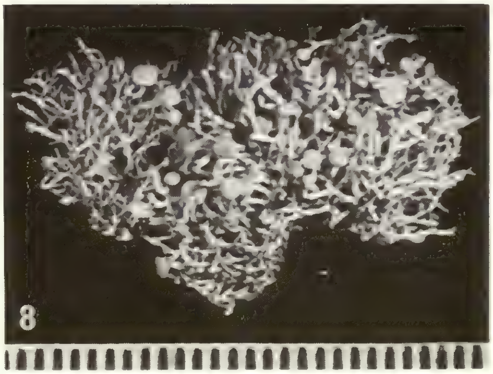
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0·5–1·0(–1·2) mm diam., plane to convex, margin entire; spores ellipsoid to fusiform, straight, 12–16(–20) × 4–6 μm (Plate 4, fig. 2).

Chemistry. Usnic acid only.

Remarks. The name *R. australiensis* as the oldest name has been upheld for this taxon, overriding the more commonly used name *R. myrioclada*. However the location given for the type material – Swan River, Western Australia – is dubious. All recent collections have been made in eastern Australia with no other material being found in the west. Whether the original material from Western Australia was wrongly recorded was not able to be ascertained.

The type material of *R. australiensis* has branchlets with black tips but this feature (as with *R. exiguella*) is not present in most specimens. The type is a coarse thallus form of this taxon, rather resembling that of the subtropical Queensland collection. There is not sufficient type material to obtain an overall picture of the total thallus.

The degree of secondary branching varies from specimen to specimen, those with dense branching resemble *R. peruviana* whereas others have sparse branching producing an open thallus form resembling the morphology of *R. filicaulis* N. Stevens.

The names *R. usneoides* and *R. usnea* have been applied to some specimens of *R. australiensis* collected in New South Wales but the Australian taxon can be distinguished by its branching pattern and subterete branches instead of the characteristic flattened branches of *R. usnea* sens. str.

Distribution and habitat. This subtropical/warm temperate maritime species does not have a

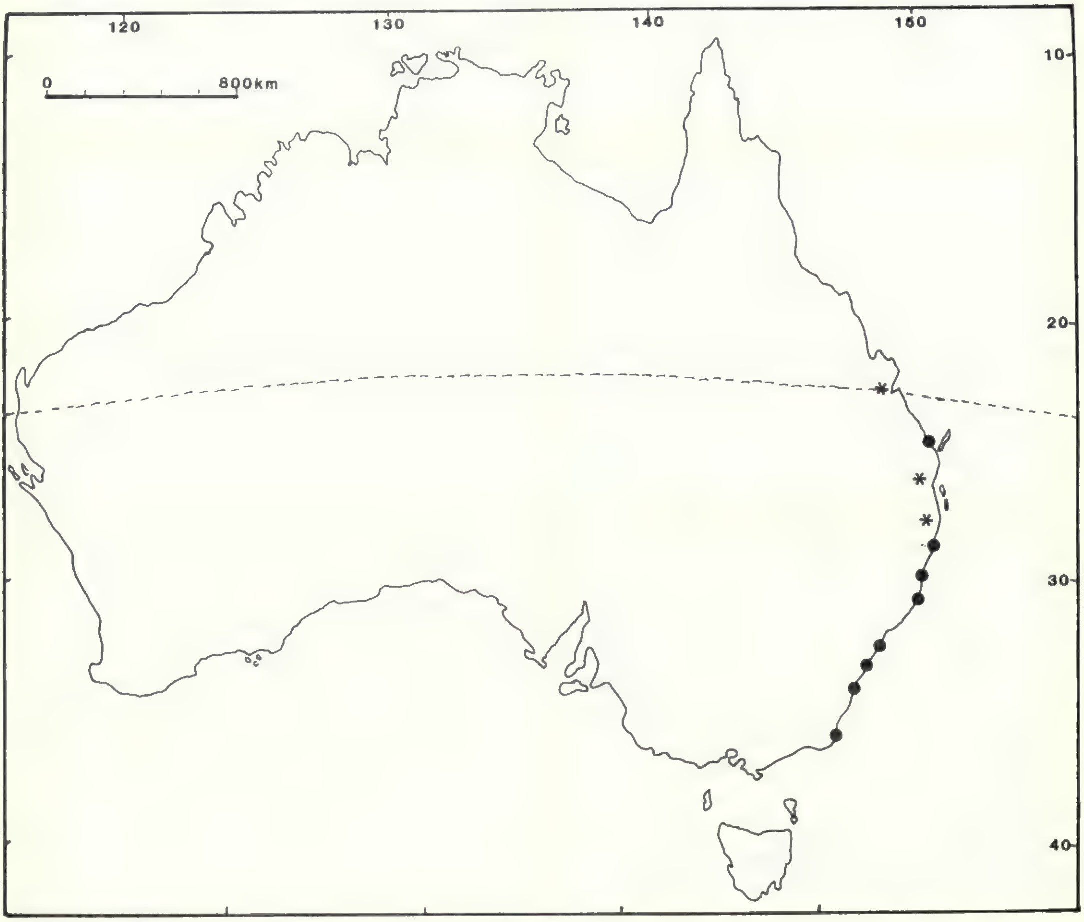

Fig. 8 Distribution of *R. australiensis* ● and *R. filicaulis* ★.

wide distribution (Fig. 8). It occurs along the coast from Yamba 29°S to Twofold Bay 37°S and has a disjunct occurrence on the Queensland coast at Toogoom (25°S). This Queensland occurrence cannot be adequately explained, although the rainfall in this area is similar to that which occurs along the New South Wales coastline. The Queensland material is extremely coarse, it was collected from *Callitris columellaris* which was growing on exposed sand dunes. The morphology of several *Ramalina* species collected from this area was also extremely coarse, indicating environmental adaptation.

The major phorophyte of *R. australiensi* is *Avicennia marina*, which grows in sheltered positions along the bays and rivers of the New South Wales coastline. However this *Ramalina* has also been collected from rocks at Port Hacking and Port Macquarie, which indicates it is not substrate specific.

This taxon occurs on the offshore islands of the North Island of New Zealand which lie at equivalent latitudes to those where *R. australiensis* occurs in Australia. The species has not been recorded anywhere else.

World distribution: Australia and New Zealand.

Queensland: Toogoom, 25°15′S, 152°40′E, on *Callitris columellaris*, 1983, *GNS* (BRIU4217NS). **New South Wales**: Yamba, 29°27′S, 153°20′E, on *Avicennia marina*, 1977, *GNS* (BRIU 1978NS); Nambucca Hds. 30°41′S, 153°00′E, on *Avicennia marina,* 1977, *GNS* (BRIU1998NS); Port Macquarie, 31°27′S, 152°55′E, on metamorphic rock, 1975, *JAE* (JAE 1081); Patonga 33°30′S, 151°20′E, on *Avicennia marina*, 1978, *GNS* (BRIU2314NS); Gosford, 33°30′S, 151°20′E, 1978, *JAE* (JAE 4715); Newport, 33°40′S, 151°20′E, on mangroves, 1888, *F. R. M. Wilson* (MEL 9409); Lilli Pilli Beach, 34°04′S, 151°10′E, on sandstone, 1975, *JAE* (JAE 1181); Sussex Inlet, 35°10′S, 150°35′E, on *Avicenna marina*, 1977, *RWR* (BRIU1902NS); Buckenbowra R. 35°42′S, 150°06′E, on *Avicennia marina* 1983, *HS* (CBG8306040); Shoalhaven R. 34°52′S, 150°42′E, on *Aegiceras corniculatum*, 1975, *P. Saenger* (BRIU2137NS).

2. ***Ramalina caespitella*** N. Stevens Plate 7, fig. 2.

in *Lichenologist* **18**: 183 (1986). Type: Australia, Long Island (Bass Strait), 1969, *Whinray* s.n. (MEL! – holotype; sekikaic acid, 4’-0-demethylsekikaic acid, ± several terpenes, and usnic acid).

Thallus saxicolous, pale greenish-grey to stramineous, minute, caespitose, rigid, up to 1·0 cm high; branching subdichotomous, irregular, narrow thalli densely branched, broad thalli sparsely branched; branch width 0·1–2·0 mm, exceptions to 6 mm, branches solid, flat to subterete, narrow branches nodular, apices broad and blunt; surface shiny; holdfast delimited or diffuse, soralia marginal and laminal, round to ellipsoidal, becoming fissural on the upper surface occurring on eroded areas of the lower surface and at the apices. Apothecia rare, laminal near the branch apices, rarely terminal, disc 1·0 mm diam, concave, margin thick, entire; spores not produced.

Chemistry: sekikaic acid (M), 4’-0-demethylsekikaic acid (t), ± several terpenes and usnic acid.

Remarks. Ramalina caespitella produces two morphotypes which intergrade into one another. One morph has narrow subterete to terete nodular branches with apical and marginal soralia, whilst the other morph produces very thick, flat to subterete branches bearing numerous soralia on both upper and lower surfaces. The extreme button-like morphology of both forms is indicative of their exposed, saxicolous habitat. No other taxon has been found to have a close affinity with *R. caespitella*.

Distribution and habitat. This temperate maritime taxon is found on several of the islands in Bass Strait and along parts of the Tasmanian coastline (Fig. 9). It occurs on siliceous rocks (e.g. granite on the islands and on quartzite or dolerite at Tasmanian locations) and often occupies cliff-face habitats.

World distribution. Australia.

Bass Strait: Hogan Group: Hogans I, 39°13′S, 146°59′E, on granite, 1973, *JW* (MEL1013070); Kents Group, Dover I, 39°29′S, 147°17′E, on granite, 1970, *JW* (MEL1012702); Deal I, 39°30′S, 147°22′E, on granite, 1972, *JW* (MEL1012940); Furneaux Group: West Sister I, 39°45′S, 147°56′E, on granite, 1966, *JW*

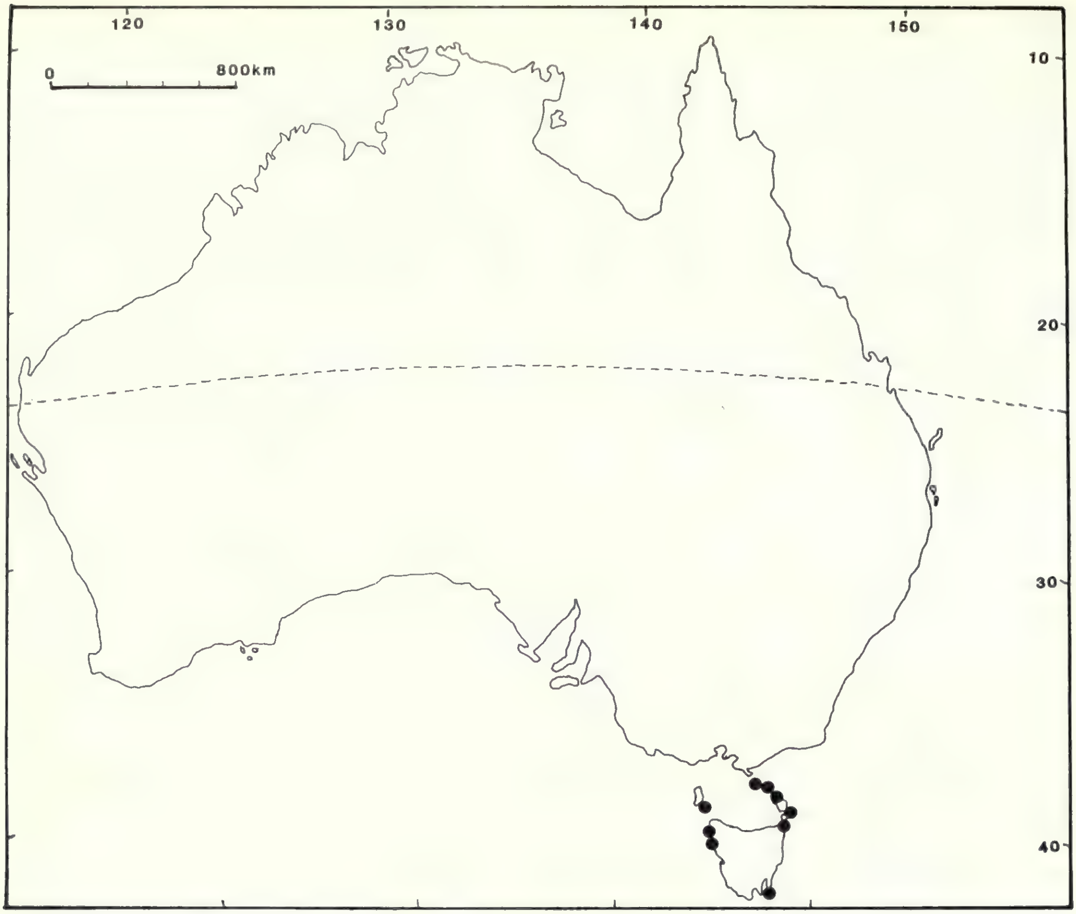

Fig. 9 Distribution of *R. caespitella*.

(MEL1026132); Cape Barren I, 40°25′S, 148°10′E, on granite, 1969, *JW* (MEL1018083); Big Chalky I, 40°06′S, 147°54′E, on granite, 1972, *JW* (MEL1018053); Isabella Reef, 40°25′S, 148°30′E, on granite 1973, *JW* (MEL522220); Flinders I, 39°45′S, 147°56′E, on rock, 1965, *RF* (MEL1026188); Swan I, 40°41′S, 148°05′E, on rock, 1974, *JW* (MEL1019119); **Tasmania**: West Point, 40°55′S, 145°15′E, on quartzite, 1981, *GK* (362/81); Rocky Cape, 40°51′S, 145°31′E, on quartzite, 1970, *GB* (H032637); Eddystone Pt., 41°00′S, 148°23′E, on granite, 1973, *GB* (H032640); Arthurs River, 41°07′S, 144°42′E, on quartzite, 1970, *GB* (H032639); Bruny I., 43°29′S, 147°09′E, on granite, 1973, *GB* (H032636).

3. ***Ramalina canariensis*** Steiner Plate 7, figs 3–4.

in *Öst. bot. Z.* **9**: 8 (1904). Type: Gran Canaria, Tafira, *Bornmüller*, Pl. Canar. 3500 (W! – isotype; divaricatic acid and usnic acid).

Thallus corticolous, pale green to grey green, erect to subpendulous, 1–3(–5) cm long; branching palmate or irregular; branch width 1–3(–10) mm, apices blunt, usually split with margins separated; surface matt, smooth to rugose, sometimes coarsely reticulately ridged by chondroid strands, pitted distally; holdfast delimited; soralia marginal and apical occurring through the separation of the upper and lower surfaces.

Apothecia not seen. Reported as rare.

Chemistry. Divaricatic acid, usnic acid.

Remarks. Fine thalli of this taxon come close to resembling immature thalli of *R. unilateralis* and both species contain divaricatic acid, but the cartilaginous surface and the finely lacerated apices of *R. unilateralis* enable the two to be separated.

Distribution and habitat. The distribution pattern of *R. canariensis* in Australia is mainly maritime in areas experiencing a Mediterranean type of climate (Fig. 10). The only inland collections are two South Australian locations (Springton and Kuitpo Forest) at elevations of 300 m where frequent mists occur.

Krog & Østhagen (1980) mentioned that in the Canary Islands (28°N) this species 'seems to prefer well lit sites with a certain influence of mist . . . between 400 and 1000 m altitude'. In some of the drier Australian coastal sites morning fogs are prevalent.

Along the southern coastline of Australia this species grows in well-lit situations protected from winds, usually on twigs of *Leucopogon parviflora, Casuarina,* and *Melaleuca* spp. It has also been found on mangroves (*Avicennia marina*) along the eastern coastline south from latitude 35°S. *Ramalina canariensis* occurs in homogeneous colonies or immixed with *R. fissa*.

Overseas specimens were examined from South Africa (Cape Province, latitude 33°S at 800 m elevation) and Chile (Valparaiso, latitude 33°S at sea level, on dune shrubs). Both of these regions have climates similar to southern Australia and other Mediterranean regions. *Ramalina canariensis* was previously thought to grow only in the northern hemisphere in the Mediterranean region and on the Canary Islands.

World distribution. Mediterranean region, Canary Islands, South Africa, Australia, and South America.

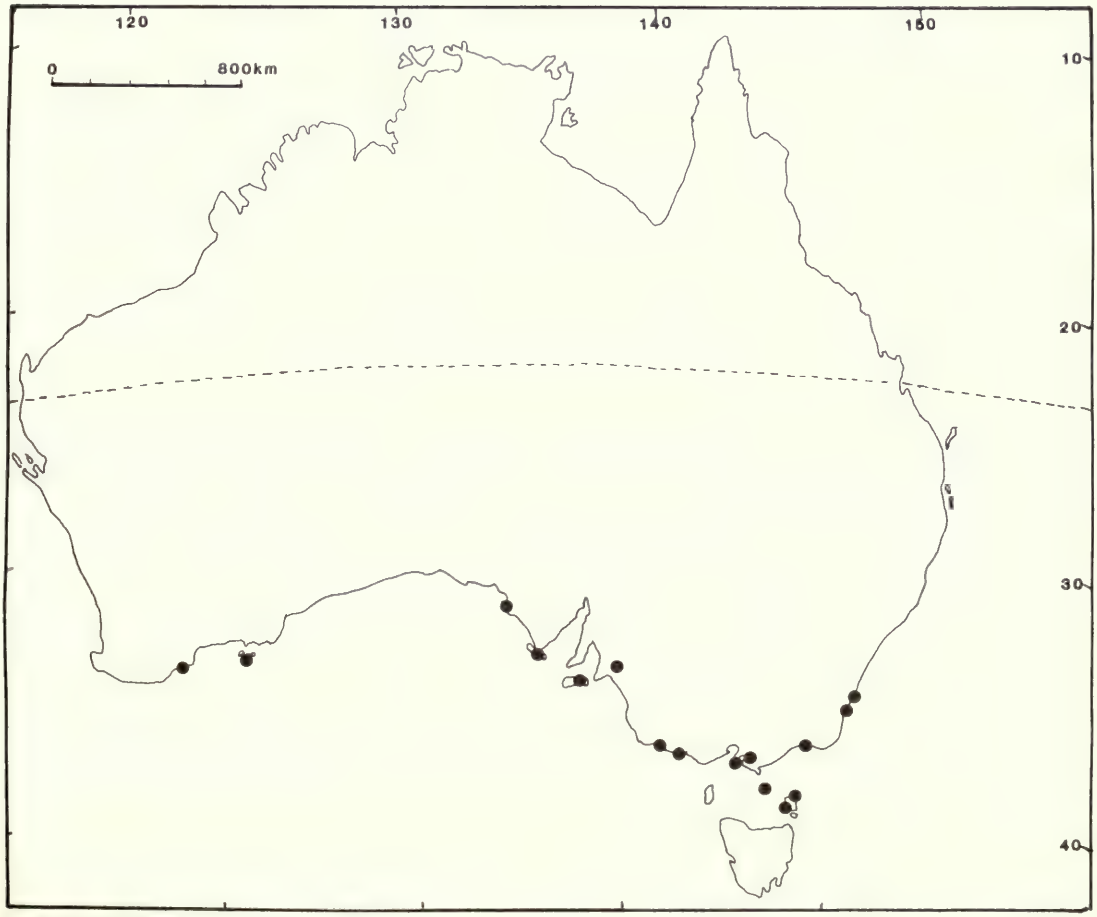

Fig. 10 Distribution of *R. canariensis*.

New South Wales: Sussex Inlet, 35°10′S, 150°35′E, on *Avicennia marina*, 1977, *RWR* (BRIU1903NS); Buckenbowra R. 35°42′S, 150°06′E, on *Avicennia marina*, 1983, *HS* (CBG8306039); Batemans Bay, 35°45′S, 150°10′E on *Avicennia marina*, 1978, *GNS* (BRIU2171NS); Batehaven Beach, 35°45′S, 150°13′E, on *Casuarina* sp., 1975, *JAE* (JAE 1061); Burrenwarra Pt., 35°49′S, 150°14′E, on *Casuaria* sp., 1975, *JAE* (JAE 1246). **Victoria**: Cape Conran, 37°48′S, 148°44′E, on *Leucopogon* sp., 1983, *GNS* (BRIU3701NS); Westernport Bay, 38°13′S, 145°18′E, on *Avicennia marina*, 1978, *GNS* (BRIU2336NS); Gunnamatta Beach, 38°21′S, 144°45′E, on *Monotoca elliptica*, 1983, *GNS* (BRIU3692NS); Warrnambool, 38°23′S, 142°29′E, 1886, *F. R. M. Wilson* (NSW.L4311); Portland, 38°20′S, 141°36′E, 1896, *F. R. M. Wilson* (MEL 9419); Portsea, 38°25′S, 144°42′E, on tree on sea cliff, 1964, *J. Williams* (MEL1026126); Somers, 38°24′S, 145°10′E, 1964, *Marie* (MEL1026173). **South Australia**: Kuitpo forest, 35°07′S, 139°16′E, on *Pinus* sp., 1968, *RWR* (BRIU1426NS); Kangaroo I. Lockwood Corner, 35°39′S, 137°38′E, 1967, *G. Jackson* (S.A.97647604); Mt Lofty Ra., Carey Gully, 34°45′, 139°00′E, on *Exocarpus cupressiformis*, 1976, *JAE* (JAE 2853); Springton, 34°45′S, 139°05′E, on *Callitris* sp., 1976. *JAE* (JAE 2807); **Eyre Peninsula**: Memory Cove, 34°40′S, 135°50′E, on *Melaleuca* sp., 1970, *RF* (MEL1018638); Elliston, 32°59′S, 134°30′E, 1967, *N. Donner* (SA97648163). **Western Australia**: Gairdner River, 34°14′S, 119°17′E, on *Hakea* sp., 1980, *D. Richardson* (WA000943); Recherche Arch. Long I, 34°03′S, 121°57′E, on *Melaleuca* sp., 1950, *JW* (MEL10020). **Bass Strait**: Furneaux Group: Flinders I, 40°00′S, 148°00′E, on shrub, 1977, *JW* (MEL10225619); East Sister I, on dune shrub, 1972, *JW* (MEL1025619); West Sister I, 39°42′S, 147°56′E, on *Pomaderris apetala*, 1969, *JW* (MEL521577); Hogan Group: Long I, 39°12′S, 147°01′E, on *Banksia integrifolia*, 1973, *JW* (MEL1012966).

4. ***Ramalina exiguella*** Stirton — Plate 7, fig. 5; Plate 13, fig. 3.

in *Trans. Proc. R. Soc. Vict.* **17**: 68 (1881). Type: Australia, Queensland, Brisbane, *Bailey* 91 (BRI! – holotype; BM – isotype; usnic acid).

Ramalina pertenuis Magnusson in *Ark. Bot.* **32A** (2): 7 (1945). Type: Oahu, Keeawa awa Valley, 1922, *Skottsberg* s.n. (GB! – part of holotype; usnic acid).

Thallus corticolous, grey-green, caespitose, erect, rigid, up to 3 cm high; branching mainly from the base, squarrose branchlets sometimes present on main branches; branch width 0·3–1·0 mm, branches subterete, narrow, apices attenuate, sometimes black tipped; cortex shiny, longitudinally grooved giving a string-like appearance; pseudocyphellae linear; holdfast delimited; soralia absent.

Apothecia few to many, usually marginal along the branches and/or subterminal causing the branch apex to become geniculate with a long, attenuate spur; disc. 0·2–2·0 mm diam., concave, plane to convex; margin entire, thick on immature apothecia; spores ovoid to ellipsoid or gibbous and slightly curved, (12–)14–16 × (5–)6–8 μm (Plate 5, fig. 1).

Chemistry. Usnic acid only.

Remarks. The affinities of this taxon lie with *R. gracilis* (Pers.) Nyl.; Nylander (1870) recorded material from Brazil, Madagascar, and Australia as belonging to *R. gracilis*. The type of *R. gracilis* was not available from either L or PC, so any relationship between these two taxa was not able to be checked. Some material of *R. gracilis* held at BM is morphologically similar to *R. exiguella* but contains salazinic acid. Krog & Swinscow (1976) reported that *R. attenuata* (Pers.) Tuck. from Domingo, resembled *R. exiguella* but contained psoromic acid. Landrón (1972) stated that *R. gracilis* contained psoromic acid whereas *R. attenuata* contained salazinic acid and that the latter species is synonymous with *R. rigida* Ach. Howe (1913–14) placed *R. rigida* and *R. gracilis* as synonyms of *R. attenuata*.

It could be that this group of taxa is a complex with several chemical races, but until the type material of all of these species can be located and examined, the relationship between these taxa cannot be resolved. Stirton stated in his type description that *R. exiguella* had affinities with *R. melanothrix* Laurer, but the latter species is quite distinct and the type material does not resemble Australian material of *R. exiguella*.

Distribution and habitat. The distribution of this coastal species is continuous along the eastern shoreline of Australia from latitudes 23°S–35°S, with additional occurrences at 18°S and 21°S. Its occurrence on the coastal hills is rare, one tropical collection was made from Abbey Peak, 650 m elevation at latitude 14°S and one subtropical collection from Mt Mothar 320 m elevation at latitude 26°S (Fig. 11).

Ramalina exiguella grows on several species of mangrove (viz. *Rhizophora stylosa, Ceriops tagal, Avicennia marina*, and *Aegiceras corniculatum*) and on other coastal trees (*Casuarina equisitifolia* and *Callitris columellaris*) which grow close to the water. It also occupies very exposed situations in the dune communities facing the ocean, where it is often the only lichen present.

This taxon shows a marked difference in size of thallus in different habitats. The thallus may be minute (1·5 cm high) and narrow (as the name implies) or extremely coarse and ropy and up to 3 cm high. South of 28°S the thalli tend to produce lateral branchlets along the branches.

In sheltered habitats, *R. exiguella* grows in association with *R. inflata* subsp. *perpusilla, R. pacifica, R. subfraxinea* var. *leiodea,* and *R. subfraxinea* var. *confirmata*.

World distribution. East Africa, Australia, and New Zealand.

Queensland: Abbey Pk 14°18′S, 144°30′E, on shrubs, 1983, *C. McCracken* (BRIU4232NS); South Mission Beach, 17°55′S, 146°05′E, on *Ficus* sp., 1983, *GNS* (BRIU4159NS); Eimeo, 21°06′S, 149°10′E, on *Cerios tagal*, 1979, *GNS* (BRIU1860NS); Yeppoon, 23°08′S, 150°45′E, on *Casuarina* sp., 1980, *RWR* (BRIU2221RR); Keppel Sands, 23°21′S, 150°47′E, on *Rhizophora stylosa*, 1975, *RWR* (BRIU890RR); Rhodds Peninsula, 24°02′S, 151°40′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1277NS); Turkey, 24°06′S, 151°37′E, on *Ceriops tagal*, 1975, *GNS* (BRIU1156NS); Round Hill Head, 24°10′S, 151°54′E, on *Aegiceras corniculatum*, 1975, *RWR* (BRIU1935RR); Burnett Heads, 24°45′S, 152°25′E, on *Casuarina*, 1976, *GNS* (BRIU4203NS); Fraser I, Wathumba Ck, 24°50′S, 153°13′E, on *Ceriops tagal*, 1975, *GNS*

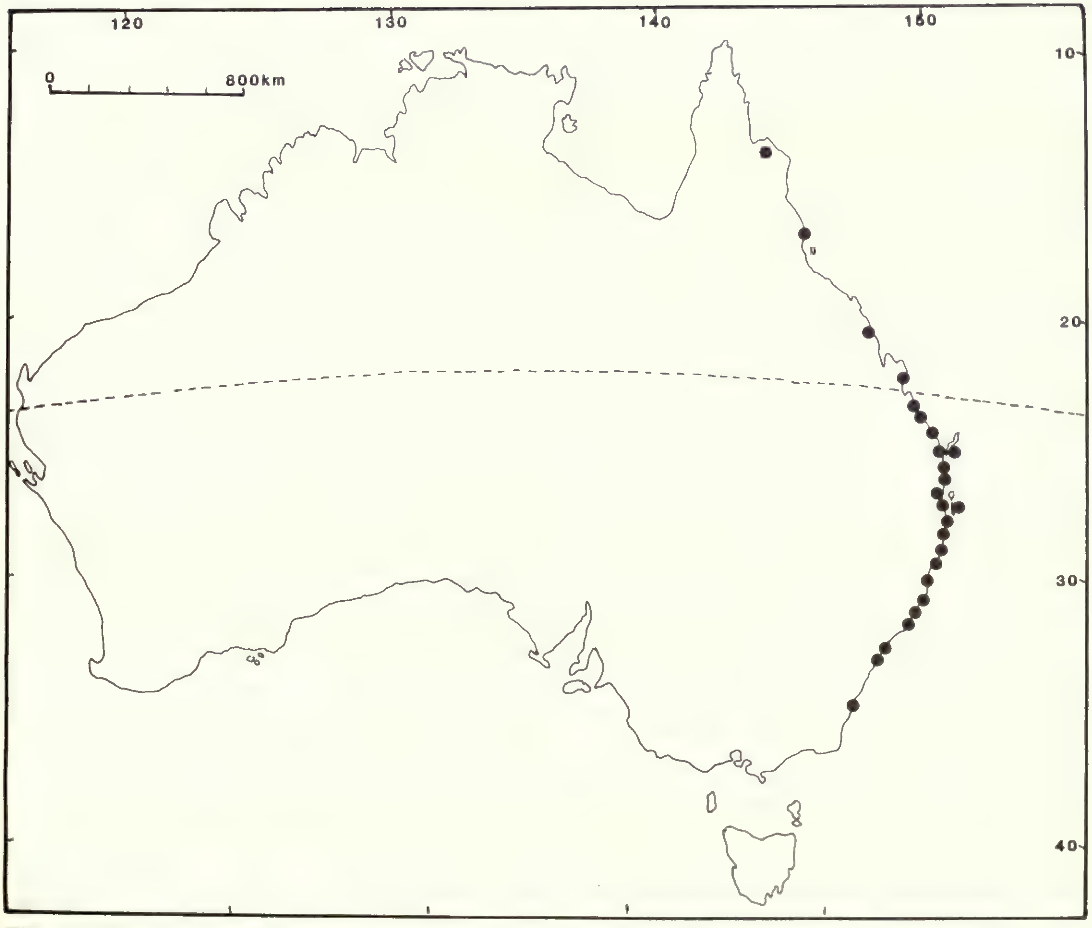

Fig. 11 Distribution of *R. exiguella*.

(BRIU642NS); Urangan, 25°19′S, 152°55′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU631NS); Boreen Point, 26°18′S, 152°58′E, on *Callitris columellaris*, 1982, *GNS* (BRIU4181NS); Cooran, 26°17′S, 152°50′E, on *Araucaria cunninghamii*, 1985, *NCS* (BRIU4335NS); Noosa River mouth, 26°24′S, 153°04′E, on *Casuarina* sp., 1980, *GNS* (BRIU3184NS); Maroochydore, Maroochy R, 26°42′S, 153°05′E, on *Avicennia marina*, 1976, *GNS* (BRIU1313NS); Currimundi Lake, 26°45′S, 153°08′E, on *Casuarina* sp., 1974, *RWR* (BRIU3078RR); Bribie I, 27°02′S, 153°10′E, on *Avicennia marina*, 1983, *GNS* (BRIU3711NS); Moreton I, Koorigal, 27°20′S, 153°25′E, on *Callitris columellaris*, 1980, *RWR* (BRIU4179NS); Stradbroke I, Myora Springs, 27°28′S, 153°24′E, on *Avicennia marina* 1977, *GNS* (BRIU1585NS); Thorneside, Tingalpa Ck 27°28′S, 153°11′E, on *Rhizophora stylosa*, 1977, *GNS* (BRIU1742NS); Wellington Point, 27°28′S, 153°15′E, on *Avicennia marina*, 1975, *RWR* (BRIU5648RR); Ormiston, 27°30′S, 153°16′E, on *Avicennia marina*, 1975, *RWR* (BRIU5459RR); Coochie Mudlo I, 27°35′S, 153°20′E, on *Callitris columellaris*, 1975, *GNS* (BRIU4579RR); Point Talburpin, 27°35′S, 153°17′E, on *Rhizophora stylosa*, 1982, *GNS* (BRIU4189NS); Little Rocky Point, 27°38′S, 153°18′E, on *Ceriops tagal*, 1977, *GNS* (BRIU1437NS). **New South Wales**: Hastings Point, 28°26′S, 153°32′E, on *Avicennia marina*, 1977, *GNS* (BRIU1929NS); Brunswick Heads, 28°33′S, 153°33′E, on *Callitris columellaris*, 1982, *GNS* (BRIU3316NS); Byron Bay, 28°40′S, 153°36′E, on *Cupaniopsis* sp., 1979, *RWR* (BRIU3179NS); Ballina, 28°54′S, 153°33′E, on *Avicennia marina*, 1977, *GNS* (BRIU1961NS); Yamba, 29°27′S, 153°20′E, on *Avicennia marina*, 1977, *GNS* (BRIU2125NS); Woolgoolga, 30°06′S, 153°12′E, on dune shrubs, 1982, *GNS* (BRIU4178NS); Sawtell, Boambee Ck, 30°22′S, 153°06′E, on *Avicennia marina*, 1977, *GNS* (BRIU2034NS); Macksville, 30°41′S, 153°00′E, on *Avicennia marina*, 1982, *GNS* (BRIU4177NS); Macleay River, 30°54′S, 153°03′E, on *Casuarina* sp., 1982, *GNS* (BRIU4175NS); Port Macquarie, 31°27′S, 152°54′E, on shrub, 1975, *JAE* (JAE 1260); Port Macquarie, 31°27′S, 152°54′E, on *Avicennia marina*, 1977, *GNS* (BRIU1983NS); Laurieton, 31°20′S, 152°55′E, on *Avicennia marina*, 1977, *GNS* (BRIU4339NS); Taree, Saltwater, 31°54′S, 152°34′E, on tree, 1977, *JAE* (JAE 4014); Booti Booti, 32°15′S, 152°31′E, on *Casuarina* sp., 1982, *GNS* (BRIU4332NS); Patonga, 33°30′S, 151°20′E, on *Avicennia marina*, 1978, *GNS* (BRIU2318NS); Towra Point, 34°03′S, 151°10′E, on *Avicennia marina*, 1977, *C. Scarlett* (BRIU641CS); Batehaven, 35°45′S, 150°10′E, on dead *Casuarina* sp., 1974, *JAE* (JAE 417).

5. ***Ramalina filicaulis*** N. Stevens, **sp. nov.** Plate 7, fig. 6.

Thallus corticolus, virido-griseus, pendulus vel decumbens usque ad 20 cm longus, ramificatione pro parte majore dichotoma; rami lati ad 0·2–0·5 mm, tenues, filicaules, subterete vel teretes, apice attenuati et filamentosi, saepe uncinatus; pagina laevigata, fere striata; soralia nulla. Apothecia rara, lateralia, disco plano vel convexo, ad 0·5–1·0 mm in diametro; sporae ellipsoideae vel fusiformes, rectae vel raro curvatae, 12–16(–20) × 4–6 μm. Acidum usnicum tantum continens.

Holotype: Australia, Queensland, Lamington Plateau, 9 km N of O'Reillys in rain-forest on *Araucaria cunninghamii*, alt. 920 m. 27 November 1983, *G. N. Stevens* 3730 (MEL 1048085!).

Thallus corticolous, green-grey, pendulous or decumbent, up to 20 cm long; branching predominantly dichotomous, curving at the axils; branches width 0·2–0·5 mm, narrow, thread-like, subterete to terete, tapering, apices attenuate and filamentous, often hooked; surface smooth, with linear pseudocyphellae; holdfast small, delimited but branches often attached to the substrate along their length; soralia absent.

Apothecia uncommon, lateral sessile, disc 0·5–1·0 mm diam., plane to convex; margin entire; spores ellipsoid to fusiform, straight or rarely curved, 12–16(–20) × 4–6 μm.

Chemistry. Usnic acid only.

Remarks. *Ramalina filicaulis* may prove to be a member of the *R. usnea* complex because, apart from a chemical difference, fine specimens of *R. filicaulis* (no medullary acids) come close to the morphology of the type material of *R. anceps* (norstictic, ± salazinic acids). Landrón (1972) recorded *R. anceps* as a species in the Caribbean Islands (10°N–21°N) that occurs in lower montane rain-forest, most abundant on trees along the edge of the forest and in areas of high rainfall.

Rundel (1978*a*) recorded that the *R. usnea* race with no medullary acids occurs most abundantly in eastern South America (23°S–28°S), a distribution pattern closely resembling the Australian taxon, but the flattened branches of *R. usnea* do not occur in *R. filicaulis*. There are morphological similarities between the Canary Island species *R. chondrina* and the Australian taxon; both are subtropical species which occur in the mountains. Krog & Østhagen (1980) recorded *R. chondrina* as sparse and scattered on trees in laurel forests between 550 and 900 m elevation at 27°30′N to 28°30′N. However, the anatomy of these two species differs; *R. chondrina* has an even cylinder of supportive tissue, whereas *R. filicaulis* has an uneven, ribbed cylinder of supportive tissue.

Distribution and habitat. This species is rare in occurrence, being known from only a few locations (Fig. 8). It occurs profusely at Jimna State Forest (26°40′S) and at Lamington Plateau (28°15′S) at elevations between 600–900 m. Two early collections may have come from lower elevations in the Rockhampton area (23°S), but little information was available on the herbarium specimens. At both Jimna and Lamington this taxon grows almost exclusively on the trunks and branches of *Araucaria cunninghamii* (hoop pine) in the rain-forest. The only other phorophyte is *Citriobatis pauciflora*, a shrub which is a remnant of the rain-forest.

The climatic data recorded for the occurrence of the hoop pine is also relevant for *R. filicaulis*. Webb & Tracey (1967) record that regions supporting *Araucaria cunninghamii* have a mean annual temperature in the subtropics between 12°–23°C, with occasional frosts; the annual average rainfall varies from 800–1800 mm with fogs and dew augmenting precipitation in upland areas. Hoop pine occurs as part of the climax forest only on soils of relatively low fertility (e.g. Jimna, on metamorphics); on soils of high fertility it does not occur in the climax forest except as rare veteran trees (e.g. Lamington Plateau, on basalt).

Because of the rarity of this *Ramalina* it is difficult to assess what environmental factors are limiting its occurrence elsewhere.

World distribution. Australia.

Queensland: Jimna, 26°40′S, 152°28′E, on *Araucaria cunninghamii*, 1980, *RWR* (BRIU2202RR); Jimna, Marumba View, 26°40′S, 152°28′E, on *Araucaria cunninghamii*, 1980, *GNS* (BRIU3349NS); Lamington Plateau, O'Reillys, 28°15′S, 153°08′E, windfall, 1970, *ED* (O); O'Reillys, 28°15′S, 153°08′E, on *Citriobatus pauciflora*, 1984, *P. Merottsy* (BRIU4344NS).

6. ***Ramalina fimbriata*** Krog & Swinscow Plate 7, fig. 7.

in *Norw. J. Bot.* **21**: 117 (1974). Type: Kenya, Central Province, Nyeri District, *Krog & Swinscow* 2K36/137 (O! – holotype; BM! – isotype; divaricatic acid and usnic acid).

Thallus saxicolous, pale green to stramineous, small, caespitose, usually very compact and button-like, often minute; up to 1·0 cm high; branching dense and intricate, distally producing branchlets; branch width 0·3–1·0 mm, branches flat to subterete, variably inflated, some branches with slit-like perforations; surface shiny to matt, smooth; holdfast diffuse; soralia form from disintegration of the lower cortex occurring laminally and at the apices (Plate 1, fig. 5).

Apothecia uncommon, but numerous on some thalli, lateral or terminal, disc 0·5–3·0 mm diam., concave, plane or convex; margin entire or incised at maturity; spores ellipsoid, straight or rarely curved, 8–13 × 4–5 μm.

Chemistry. Divaricatic acid (often in trace amounts).

Remarks. Reduced forms of *R. unilateralis* come close to the morphology of *R. fimbriata*, but the former species is corticolous in Australia and shows no inflation of the branches. The northern hemisphere species *R. pollinaria*, when growing on rock, produces thalli closely resembling *R. fimbriata*, but the former produces evernic acid. It is suggested that convergence of morphology due to similarity of habitats is the reason for the resemblance.

Distribution and habitat. Ramalina fimbriata has a distribution range from latitude 35°S–43°S over most of the Victorian highlands extending into eastern Tasmania (Fig. 12). In Australia this species is saxicolous only, although in East Africa it is both saxicolous and corticolous (Krog & Swinscow, 1974).

Its occurrence on several types of rock (viz. granite, sandstone, conglomerate, trachyte, and dolerite) shows it is not substrate specific. In some localities *R. fimbriata* occupies sheltered overhangs and ledges, habitats which would have little moisture available for the thalli, apart

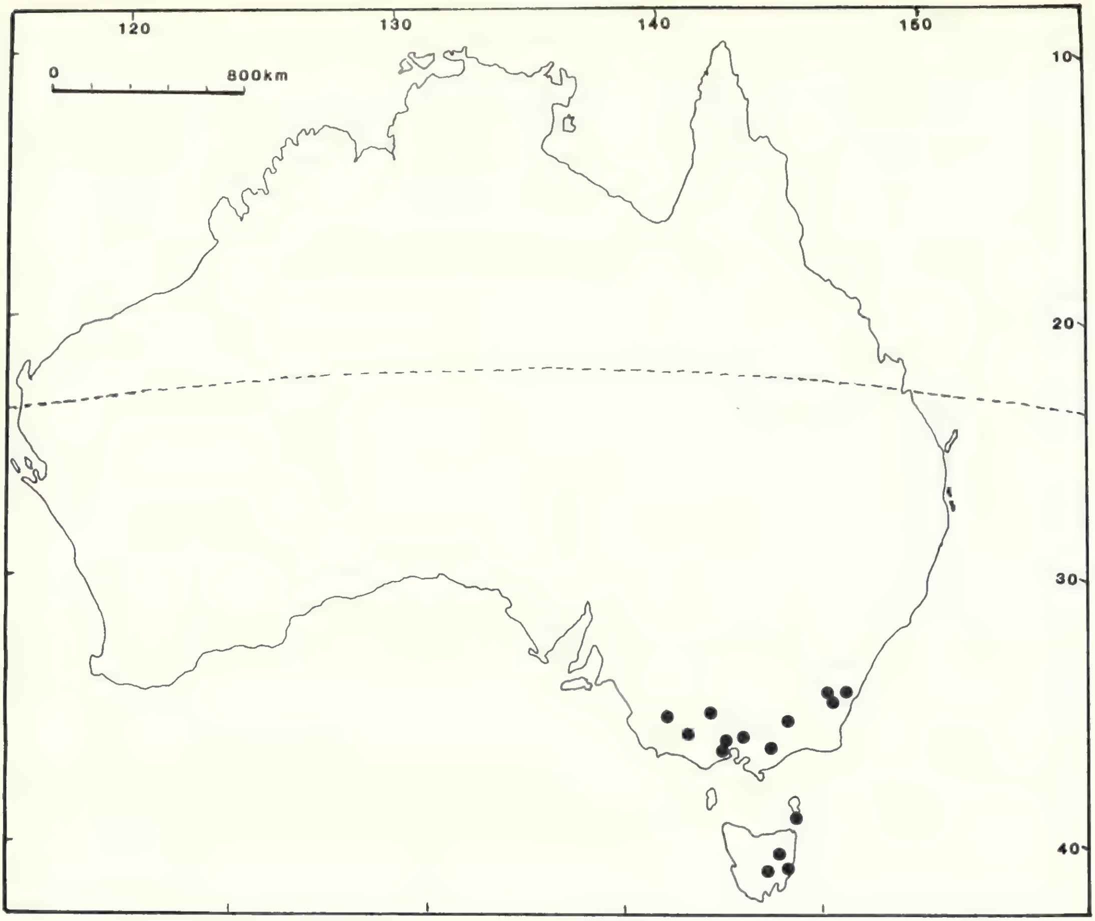

Fig. 12 Distribution of *R. fimbriata*.

from vapour or water droplets from the overhang. Yet large monotypic populations are found in such habitats. Fertile specimens were found at Mt Arapiles under a rock overhang. The production of apothecia in this sorediate species is rare and the ascospores were produced only sparingly, so that mature spores were hard to find.

Other habitats where this species occurs are exposed rock surfaces where the small thalli are further reduced in size, indicating the harsh environmental conditions prevailing (e.g. cold winter temperatures with frosts and/or snow and hot summer temperatures). Krog & Swinscow (1974) record *R. fimbriata* growing on rock in the alpine zone of East Africa at altitudes of 3200–4100 m.

The compact button-like thalli commonly collected in Australia are smaller than the corticolous Kenyan material recorded by Krog & Swinscow (1974), but in all other characteristics they are identical.

World distribution. Africa, Australia, and New Zealand.

New South Wales: Budawang Ra. 35°22′S, 150°03′E, on conglomerate, 1981, *W. A. Weber* (COLO 616); **Australian Capital Territory**: Tharwa, 11 km SW of, 35°31′S, 149°04′E, on granite, 1979, *JAE* (JAE 6195); Booroomba Rocks, 35°32′S, 149°00′E, on granite, 1979, *HS* (CBG7910804); Mt Clear, 35°43′S, 149°07′E, on granite, 1980, *JAE* (JAE 9013). **Victoria**: Mt Arapiles, 36°45′S, 141°50′E, on sandstone, 1981, *RWR* (BRIU2420RR); 1969, *A. C. Beauglehole* (MEL1013299); Melville Caves Park, 36°39′S, 143°42′E, on rock, 1964, *RF* (MEL1516515); Bogong High Plains, 36°44′S, 147°18′E, on rock, 1954, *C. Skewes* (MEL1025567); Mt Ararat, 37°20′S, 142°52′E, *c.* 1875, *D. Sullivan* (MEL 9471); Hanging Rock, 37°23′S, 144°37′E, on trachyte, 1976, *GNS* (BRIU3127NS); Yea, 37°13′S, 145°26′E, on granite, 1964, *RF* (MEL1026128); You Yangs, 38°00′S, 144°29′E, on granite, 1966, *GB* (H032638). **Tasmania**: Avoca, 41°45′S, 147°42′E, on granite, 1972, *GB* (H032552); Freycinet National Park, Mt Amos, 42°13′S, 148°18′E, on granite, 1979, *JAE* (JAE 5522); Woods Quoin, 42°16′S, 147°05′E, on dolerite, 1972, *GB & JC* (H032336); Lake Tooms Rd, 42°20′S, 147°28′E, on rock, 1974, *GB & JC* (H032551).

7. ***Ramalina glaucescens*** Krempelh. Plate 8, figs 1–12; Plate 13, fig. 4.

in *Verh. zool.-bot. Ges. Wien* **30**: 333 (1880). Type: Australia, Victoria, Mount Ararat, 1875, *Sullivan* s.n. (M! – holotype; sekikaic acid and usnic acid).

Ramalina leiodea var. *fastigiatula* Müll. Arg. in *Flora, Jena* **66**: 21 (1883). Type: Australia, Victoria, The Grampians, *Sullivan* 14 (G! – holotype; sekikaic acid (trace) and usnic acid). Plate 13, fig. 6.

Ramalina lacerata Müll. Arg. in *Flora, Jena* **66**: 20 (1883). Type: Australia, Western Australia, Eucla, *Oliver* s.n. (G! – holotype; M!, MEL!, UPS! – isotypes; no medullary acids usnic acid only). Plate 13, fig. 5.

Ramalina brevis F. Wilson in *Victorian Nat.* **6**: 69 (1889). Type: Australia, Victoria, Warrnambool, 1887, *F. R. M. Wilson* s.n. (NSW! – holotype (L4091); no medullary acids, usnic acid only). Plate 13, fig. 8.

Ramalina calicaris var. *australica* Räsänen in *Suomal. eläin-ja kasvit. Seur. van. Tiedon. Pöytäk.* **4**: 178 (1949). Type: Australia, Victoria, Barwon Heads, 1894, *F. R. M. Wilson* s.n. (H! (herb. Räsänen) – holotype; no medullary acids, usnic acid only). Plate 13, fig. 7.

Thallus corticolous, pale green, caespitose, erect to subpendulous, up to 4 cm long, exceptions to 6 cm; branching sparse, subdichotomous to irregular, additional side branchlets occur on narrow branches; branch width (0·5–)1–5(–10) mm, branches compressed, narrow and canaliculate or broad and flat, apices usually forked, narrow branches with fine pointed apices broad branches with dissected apices; surface shiny and smooth or matt and rugose, becoming coarse with chondroid strands showing at the surface, often horny in texture; holdfast delimited or diffuse (if growing in colonies); soralia absent.

Apothecia common, laminal at the axil of bifurcating branches (to 5 mm diam.) or laminal towards the branch apices (0·5–1·0 mm diam.), marginal and subterminal on narrow canaliculate branches (0·5–1·5 mm diam.), laminal on broad branches (2–10 mm diam.) at or near the apex margin, with smaller apothecia on the same branch near the centre; disc concave becoming plane, rarely convex; margin thick to thin, persistent, often inrolled; spores ellipsoid, straight or curved, 10–12(–16) × 4–5(–6) μm.

Chemistry. Sekikaic acid (± trace homosekikaic acid or trace divaricatic acid), or usnic acid only, or divaricatic acid and usnic acid.

Remarks. The type material of *R. glaucescens* comprises a branch covered with tiny tufted specimens and a card with four specimens attached to it (which are here designated a, b, c, d). Two growth forms are represented on the card; a and d have bifurcate branches with small apothecia lying at the axil of the fork, and b and c have broader branches and bear terminal or subterminal apothecia, the latter with small subtending spurs. All of the thalli tested contain sekikaic acid. The specimens are exceptionally small and are immature.

The considerable polymorphism encountered in *R. glaucescens* presented much difficulty in interpretation, as there was no correlation with the chemical variation; a situation rather similar to that encountered by Kristinsson (1969) in dealing with *Cetraria islandica* in Iceland. Five different species names already existed for entities now included in the complex: *R. glaucescens* Krempelh., *R. leiodea* var. *fastigiatula* Müll. Arg., *R. brevis* F. Wilson, *R. lacerata* Müll. Arg., and *R. calicaris* var. *australica* Räsänen. After the examination of large quantities of material belonging to this complex, both in the field and from herbarium collections, it became obvious that the four names additional to that of *R. glaucescens* (the earliest name) could not be maintained as species, because of the subtle intergradation between each of them (Plate 8, figs 1–15).

An examination of spores from all of the morphotypes failed to show any marked differences in spore size or shape. Each apothecium produced spores with considerable variation in both

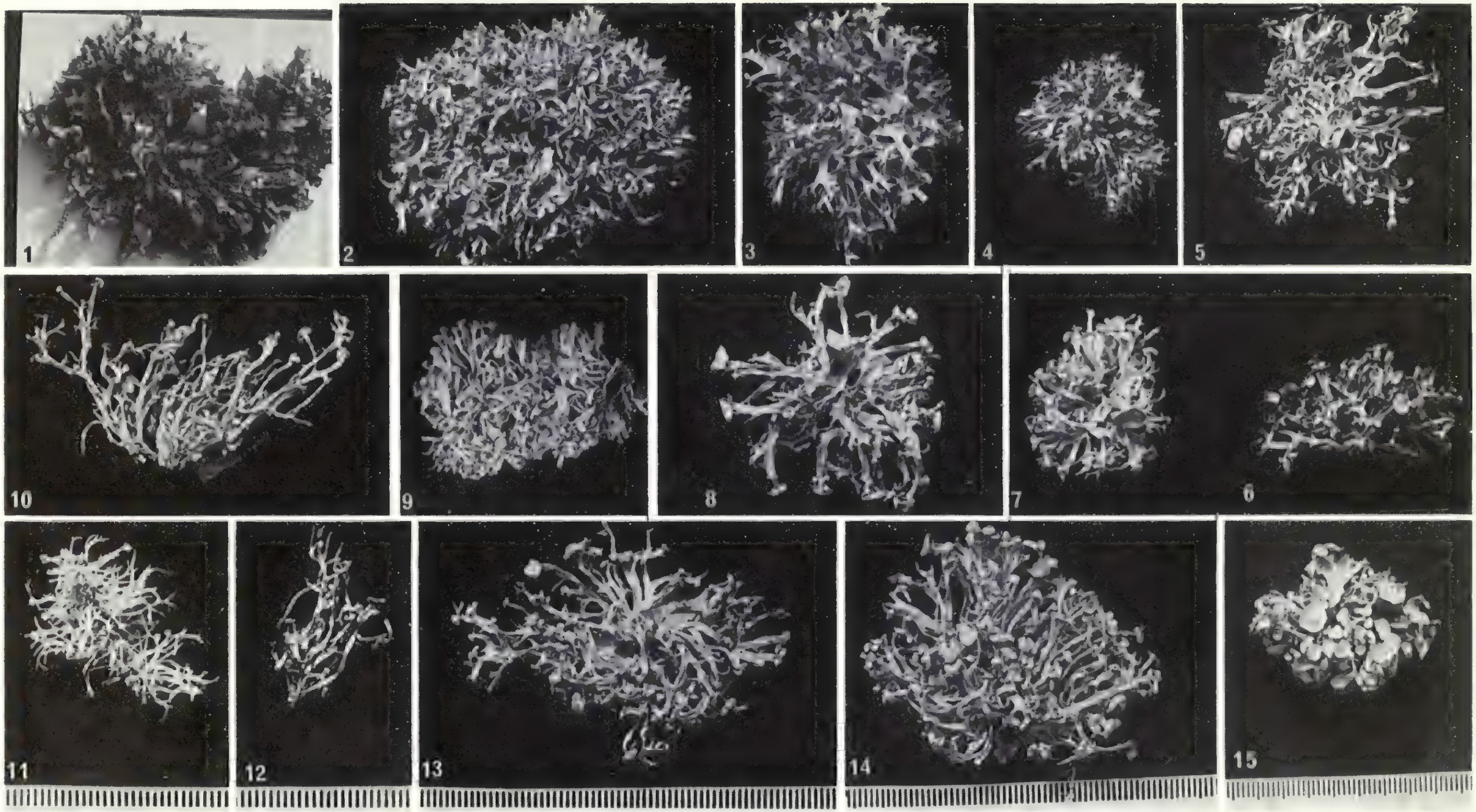

Plate 8 Fifteen morphotypes of *R. glaucescens* set out in multi-directional array, showing morphological variation. All to same scale in mm. Fig. 4 resembles the type of *R. glaucescens*. Fig. 5 resembles the type of *R. lacerata*. Fig. 8 resembles the type of *R. calicaris* var. *australica*. Fig. 9 resembles the type of *R. leiodea* var. *fastigiatula*. Fig. 15 resembles the type of *R. brevis*.

characters, so that the ratio of breadth to length was never constant for any particular morphotype. The ratio of straight to bent spores was also variable with a tendency towards a greater proportion of bent spores in the coastal thalli.

The taxonomic interpretation of this complexity of morphotypes offered two alternatives: (1) to regard each existing ecotype as a distinct species which would allow for the five existing species and would produce at least two other new taxa, or (2) to regard the whole group as one extremely variable species showing remarkable phenotypic plasticity in response to environmental pressures. The latter would incorporate numerous morphotypes with similar spores and anatomy, which occupied different habitats, yet showed intergradation between their extreme morphological forms (Plate 8, figs 1–15). The second alternative was chosen because variation in chemistry also occurs throughout the group, which made it impossible to satisfactorily find any point for delimitation based on the acids present.

Consideration was given to applying varietal rank to the different ecotypes, but each ecotype would then have had a sekikaic acid race and an acid-deficient race. The division of *R. glaucescens* into two taxa based on presence or absence of medullary acids could be feasible, especially as thalli containing sekikaic acid occur mainly east of longitude 147°, whereas west of this latitude the majority of the specimens contain no acids. If a division of taxa was made this way then a mixed group of morphotypes would be placed in each class. The amount of sekikaic acid present in *R. glaucescens* specimens is very variable in quantity, and division of a species on so fine a difference as presence or absence of traces of sekikaic acid appeared unwarranted. Usually acid-deficient races are not distinguished taxonomically from their acid-producing partners.

The extreme variability of this taxon (as described above) indicates it could be a rapidly expanding species in Australia. As it also occurs in New Zealand, investigation of material here may provide information to clarify how it should be divided, whether on its chemistry or its morphology. Until the matter is finally resolved this complex of morphotypes is regarded as a single, markedly polymorphic species.

Two specimens collected from Walcha Road (31°S) contain divaricatic acid; and both sekikaic and divaricatic acids occur in several thalli collected at Nimmitabel (36°S); this anomaly cannot be explained. Both areas are at altitudes of over 1000 m and such habitats may produce physiological changes in the metabolism of *R. glaucescens*. No taxonomic rank was considered for the atypical divaricatic acid thalli.

Distribution and habitat. Ramalina glaucescens has a wide distribution in the warm to cool temperate regions of eastern Australia (Fig. 13), occurring at altitudes from sea level to over 1300 m. A large number of morphotypes are found as illustrated in Plate 8, figs 1–15. A general intergradation of forms can be seen which do not form a continuum but merge from several directions.

Thalli with a morphology which is larger, but otherwise similar to that of the type of *R. glaucescens*, are found along the inland mountains west of the eastern escarpment in New South Wales and in the mountainous area of central Victoria, as well as in the central and eastern mountains of Tasmania (Plate 8, figs 2, 3, 4, 5). All of the specimens examined contain sekikaic acid in varying amounts, except for a few from western Victoria and South Australia which are acid-deficient.

Intergrading with this morphotype is a narrower, sometimes canaliculate morph which often has subsidiary branchlets extending from the main branches; it has both terminal and subterminal apothecia. The distribution of this ecotype is in the Eastern Highlands (with a disjunct appearance in the Grampians – type location of *R. leiodea* var. *fastigiatula*) and in the highlands of Tasmania (Plate 8, figs 5, 6, 7, 9, 13, 14). In its narrowest form the branches become subterete and very fine, bearing small apothecia; the apices of the branches are sharply pointed (Plate 8, figs 11, 12); this spiky form occurs in mountain habitats above 1400 m elevation in the temperate region, e.g. it occurs at Mt Aggie and the Brindabella Ranges in New South Wales and at Mt Wombargo in Victoria, and at lower altitudes at Buchan Caves, Victoria, and in Tasmania. All collections were from twigs of Epacridaceae bushes, so it is not clear whether low temperatures

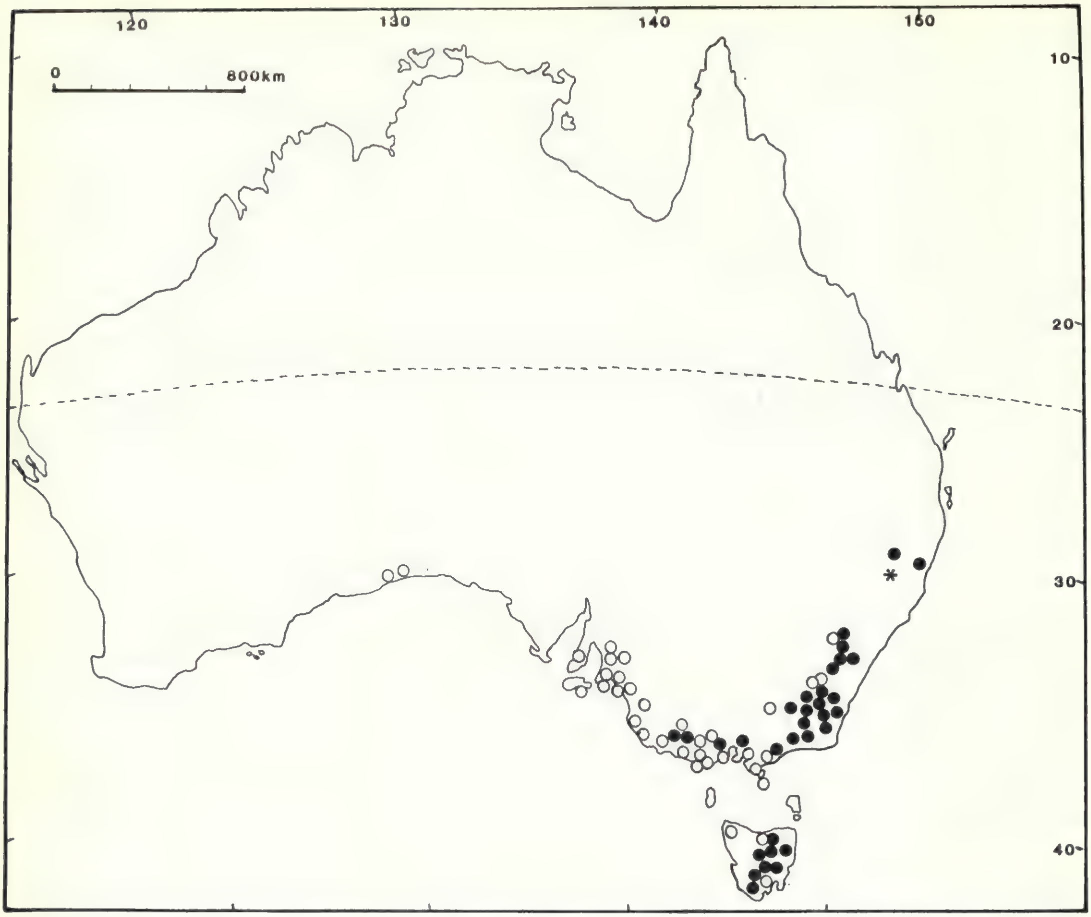

Fig. 13 Distribution of *R. glaucescens:* ● sekikaic acid race; ○ acid-deficient race; ★ divaricatic acid race.

or a particular bark substrate has an effect on this phenotype's distribution. Sekikaic acid was always present in such thalli.

One ecotype of *R. glaucescens* grows along the southern Victorian coastline; it has a short broad thallus with large terminal or laminal apothecia and is acid-deficient. A few specimens resembling this morphology have been collected from inland in eastern Australia, but that material contains sekikaic acid and is not so coarsely textured as the coastal thalli. This ecotype resembles the type of *R. brevis* (Plate 8, fig. 15).

Another acid-deficient ecotype occurs inland at low altitudes in Victoria and South Australia, but the thallus is generally narrower than that of the coastal ecotype and the apothecia are not as large; however, intergradation between the two is evident at some locations (Plate 8, fig. 8). The presence of small branchlets on the main branches resembles the eastern highlands ecotype. The type of *R. calicaris* var. *australica* belongs to this ecotype. In some habitats the thallus becomes quite coarse in texture with chondroid strands showing at the surface; such characteristics are apparent in the material from the arid zone in Western Australia, including the type collection of *R. lacerata*.

The largest morphotype in the *R. glaucescens* complex is found in western Victoria and eastern South Australia, with a few specimens collected in western New South Wales. The latter specimens contain sekikaic acid but all other material proved to be acid-deficient. Most of the ecotypes of *R. glaucescens* have been found to intergrade with this large morphotype (Plate 8, fig. 1). It is normally sterile although pycnidia have been detected in some of these specimens.

Four of the type specimens here included in *R. glaucescens* were initially collected within 100 km radius of one another in Victoria, which illustrates the ecophenotypic response to different habitats. Table 9 summarises the morphological variation that is found in the different ecotypes.

This taxon is entirely corticolous, the most common phorophytes being *Acacia* spp. and *Bursaria spinosa*. It occurs as dense colonies along the branches of isolated trees in pastureland or in open-forest communities. In some localities the entire population may be small and immature (as found in the type material of both *R. glaucescens* and *R. leiodea* var. *fastigiatula*), whereas in other areas only large mature specimens occur.

World distribution. Australia and New Zealand.

New South Wales: Ben Lomond, 30°00′S, 151°42′E, on *Acacia* sp., 1980, *GNS* (BRIU3249NS); Sherwood Ck, 30°03′S, 153°03′E, on lemon tree, 1978, *HS* (CBG7905095); Walcha, 10 km W of, 30°58′S, 151°30′E, on *Acacia* sp., 1982, *GNS* (BRIU4100NS); Abercrombie Caves, 33°32′S, 149°15′S, on *Leptospermum* sp., 1978, *JAE* (JAE 4640); Rockley, 33°42′S, 149°34′E, *E. Boorman* (G); Black Springs 10 km N of, 33°49′S, 149°48′E, on *Acacia* sp., 1984, *NCS* (BRIU4292NS); Black Springs 5 km S of, 33°52′S, 149°48′E, on *Acacia* sp., 1984, *NCS* (BRIU4283NS); Abercrombie R. 34°12′S, 149°45′E, on *Pinus* sp., 1984, *NCS* (BRIU4284NS); Wombeyan Caves, 34°18′S, 150°02′E, *E. Cheel* (NSW L4294); Taralga, 37 km N of, 34°24′S, 149°49′E, on fence posts, 1977, *JAE* (JAE 3165); Crookwell, 34°28′S, 149°30′E, on *Acacia* sp., 1980, *GNS* (BRIU3489NS); Yass, 26 km S of, 35°00′S, 148°50′E, on *Casuarina* sp., 1975, *HS* (CBG058278); Little Peppercorn Ck, 35°35′S, 148°37′E, on *Bursaria spinosa*, 1979, *HS* (CBG7906928); Rules Point, 35°43′S, 148°31′E, on shrub, 1979, *HS* (CBG7907045); Lake Eucumbene, 36°10′S, 148°50′E, on *Hymenanthera* sp., 1971, *L. Craven* (MEL1020182); Adaminaby, 36°12′S, 148°50′E, on Briar, 1984, *NCS* (BRIU4287NS); Countegany, 36°12′S, 149°29′E, on *Acacia melanoxylon*, 1976, *JAE* (JAE 1925); Cooma 46 km S of, 36°14′S, 149°05′E, on *Acacia* sp., 1978, *JAE* (JAE 5440); Nimmitabel, 36°31′S, 149°15′E, on *Prunus* sp., 1980, *GNS* (BRIU3215NS); Holts Flat, 36°40′S, 149°15′E, on *Acacia* sp., 1980, *GNS* (BRIU3310NS); Delegate, 37°03′S, 148°57′E, on *Acacia* sp., 1980, *GNS* (BRIU3490NS). **Australian Capital Territory**: Ginninderra Ck, 35°05′S, 149°03′E, 1977, *HS* (CBG066912); Uriarra Crossing, 35°08′S, 148°57′E, on *Casuarina* sp., 1974, *JAE* (JAE 628); Blundells Ck Rd., 35°21′S, 148°50′E, on *Acacia* sp., 1977, *D. Verdon* (CBG8008538); Mt Aggie, 35°27′S, 148°46′E, on *Hymenanthera dentata*, 1979, *JAE* (JAE 5870). **Victoria**: Walwa, 9 km S of, 35°55′S, 147°45′E, on *Acacia* sp., 1984, *NCS* (BRIU4338NS); SW of Corryong, 36°16′S, 146°50′E, on Briar, 1984, *NCS* (BRIU4288NS); Myrtleford, 19 km S of, 36°39′S, 146°42′E, on *Acacia* sp., 1984, *NCS* (BRIU4290NS); Tawonga, 36°41′S, 147°08′E, on *Prunus* sp., 1984, *NCS* (BRIU4293NS); Bright, 36°44′S, 146°58′E, on copper beech, 1984, *NCS* (BRIU4286NS); Mt Wombergo, 36°36′S, 148°11′S, on *Hymenanthera* sp., 1966, *RF*. (MEL1026138); Bonang, 37°12′S, 148°43′E, on *Malus*, 1980, *GNS* (BRIU3491NS); Kyneton, 37°15′S, 144°28′E, 1897, *F. R. M. Wilson*, (MEL 9440); Newlyn, 37°25′S, 144°00′E, on *Crataegus* sp., 1981, *RWR* (BRIU2334RR); Buchan Caves, 37°30′S, 148°10′E, 1965, *RF* (MEL1026151); Omeo, 7 km N of, 37°04′S, 147°38′E, on *Acacia* sp., 1984, *NCS* (BRIU4285NS); Skipton, 11 km S of, 37°47′S, 143°22′E, on *Hymenanthera* sp., 1984, *NCS* (BRIU4291NS); Buninyong, 37°42′S, 143°40′E, on trees, *F. R. M. Wilson* (MEL 9479); Steiglitz, Moorabool R dam, 37°53′S, 144°11′E, on twigs, 1968, *GB* (H032786); Yallourn, Storage dam, 38°10′S, 146°20′E, 1975, *RF* (MEL1013745); Koweerup, 12 km NE of, 38°10′S, 145°36′E, on *Pinus* sp., 1984, *NCS* (BRIU4336NS); Loy Yang, 38°11′S, 146°37′E, on *Acacia* sp., 1984, *NCS* (BRIU4337NS); Billywing Forest, 37°10′S, 142°10′E, *Acacia baileyi*, 1981, *RWR* (BRIU2429RR); Dartmoor, Crawford Lake, 37°56′S, 141°25′E, 1978, *T. Muir* (MEL1025115); Macarthur, 16 km W of, 37°58′S, 141°48′E, on *Leptospermum* sp., 1969, *A. Orchard* (SA97647210); Sale, 38°07′S, 147°04′E, on *Acacia* sp., 1980, *GNS* (BRIU3208NS); Tyrendarra, 38°15′S, 141°50′E, on tree, 1951, *A. C. Beauglehole* (MEL 9487); Lake Beeac, 38°12′S, 143°38′E, on Briar, 1984, *NCS* (BRIU4340NS); Barwon Hds, 38°20′S, 144°30′E, 1894, *F. R. M. Wilson* (H); Gunnamatta Beach, 38°20′S, 144°45′E, on *Pimelea* sp., 1983, *GNS* (BRIU3680NS); Strzelecki South, 38°20′S, 145°58′E, on dead wood, 1971, *GB & JC* (H032630); Westernport Bay, 38°22′S, 145°20′E, on *Avicennia marina*, 1978, *GNS* (BRIU4250NS); Warrnambool, 38°23′S, 142°31′E, on *Bursaria spinosa*, 1887, *F. R. M. Wilson* (NSW L4091); Pirron Yalook, 38°21′S, 143°26′E, on shrub, 1952, *A. C. Beauglehole* (MEL1023376); Yarram, 17 km NNW of, 38°24′S, 146°38′E, on *Acacia* sp., 1980, *HS* (CBG8002966); Korumburra, 38°26′S, 145°49′E, on *Acacia* sp., 1980, *GNS* (BRIU3301NS); Forrest, upper Barwon R, 38°32′S, 143°45′E, on ‘prickly moses’ bush, 1952, *A. C. Beauglehole* (MEL1023362); Gellibrand R. falls, 38°40′S, 143°10′E, on tree, 1952, *A. C. Beauglehole* (MEL1023385); Skenes Ck, 38°43′S, 143°45′E, on *Helicrysum dendroideum*, 1983, *M. Seaward* 104633; Wilsons Promontary, 39°06′S, 146°12′E, on *Acacia* sp., 1980, *GNS* (BRIU3207NS). **South Australia**: Yalata Roadhouse, 31°39′S, 129°03′E, on bushes, 1980, *AA* (BRIU4341NS); Swan Reach, 24 km S of, 34°37′S, 139°30′E, 1971, *K. Czornij* (SA97414420); Springton, 6 km W of, 34°39′S, 139°06′E, on *Hakea* sp., 1975, *JAE* (JAE 884);

Table 9 Geographic segregation of the polymorphic *Ramalina glaucescens* showing variation in the morphological and chemical characters of the ecotypes.

Geographical area	Acid present	Branch length cm	Branch width mm	Branch shape & apices	Texture of cortex	Position of apothecia	Disc shape	Diam. of apothecia	Spores
Eastern Highlands to central west Victoria	sekikaic mainly, few nil	1–3	1–5	flat, apices forked	matt, coarse rugose	laminal	concave to plane	0·5–8	(10–)12–16 × 4–6 μm straight 50% curved 50%
Coastal Victoria	nil	2	2–8	flat, apices broad	coarse with reticulate wrinkles	laminal and terminal	concave to plane	1–8	12–14(–16) × 4–5(–6) μm straight 20% curved 80%
South-west Victoria and South Australia (dry areas)	nil with few sekikaic	5	2–8	flat, apices often tattered	matt, rugose ridged	laminal	concave to plane	1–5	12–14 × 4–5 μm straight 70% curved 30%
Eastern Highlands (high altitudes) to central west Victoria	sekikaic mainly few nil	1–3	0·5–2	narrow canaliculate apices forked	shiny, smooth	subterminal and marginal	concave to plane	1–2	(10–)12–16 × 4–5 μm straight 50% curved 50%
South-west Victoria and South Australia	nil	2–4	2–4	flat to slightly canaliculate	matt, smooth coarse	terminal and subterminal	concave plane to convex	1–3	12–16 × 4–5(–6) μm straight 50% curved 50%
West Australia (Eucla – arid region)	nil	2–3	1–1·5	narrow canaliculate apices tattered	shiny, coarse	terminal and subterminal	concave to plane	1–3	12–16 × 4–6 μm — —

Curramulka 5 km W of, 34°43′S, 137°45′E, on *Casuarina* sp., 1977, *JAE* (JAE 3731); Kuitpo Forest, 35°14′S, 138°36′E, windfall, 1968, *RWR* (BRIU3032RR); Myponga, 35°24′S, 138°28′E, 1968, *V. Cruickshank* (SA97414419); Clarendon, 35°06′S, 138°40′E, 1968, *V. Cruickshank* (SA97418422); Strathalbyn, 35°20′S, 138°50′E, 1968, *V. Cruickshank* (SA97414424); Salt Ck, 35°28′S, 139°09′E, on dead gum, 1967, *GB* (H032783); Deep Ck, 35°38′S, 138°12′E, on *Casuarina* sp., 1979, *RWR* (BRIU1863RR); Messent N.P., 35°28′S, 139°10′E, 1969, *J. Carrick* (SA97416171); Hindmarsh Falls, 35°29′S, 138°38′E, 1968, *V. Cruickshank* (SA97416168); Kangaroo I. Lockwood Cnr. 35°39′S, 137°38′E, on tree, 1967, *G. Jackson* (SA97647604); The Gap, 36°41′S, 140°40′E, 1973, *M. Beck* (H032671); Kingston, 60 km N of, 36°50′S, 139°51′E, *P. Copley* (SA97648420); Milbrook Reservoir, 34°50′S, 138°47′E, on *Hakea* sp., 1969, *RWR* (BRIU1780RR); Penola, 37°23′S, 140°49′E, on twigs, 1971, *RWR* (BRIU2035RR). **Western Australia**: Eucla, 31°43′S, 128°55′E, *J. Oliver* (G, M). **Tasmania**: Trowutta, 41°02′S, 145°05′E, on *Malus* sp., 1981, *GK* 384/81; Beaconfield, 41°12′S, 146°45′E, on *Acacia dealbata*, 1980, *GK* 214/80; Prossers Forest Rd, 41°15′S, 147°18′E, on *Malus* sp., 1966, *GB* (H032777); Avoca, Lochaver, 41°41′S, 147°50′E, on *Prunus* sp., 1978, *GK* 1/78; Cressy, 41°43′S, 147°02′E, on dead *Acacia*, 1964, *JC* (H032576); Lake Augusta, 41°50′S, 146°34′E, on twigs, 1973, *GB* (H032591); Great Lake Plateau, 41°57′S, 146°40′E, on bush, 1969, *GB* (H032628); Macquarie R, 42°08′S, 147°33′E, on small bushes, 1966, *GB & JC* (H032780); Lake Tooms Rd, 42°20′S, 147°28′E, on small bushes, 1974, *GB & Gilbert*, (H032791); Bothwell, 42°23′S, 147°00′E, 1968, *GB & JC* (H032593); Spring Hill, 42°24′S, 147°15′E, 1963, *GB* (H032770); Clyde Valley, 42°27′S, 146°52′E, on *Acacia* sp., 1975, *K. Davies* (H032629); Ouse, 42°28′S, 146°44′E, on *Malus* sp., 1980, *GNS* (BRIU3340NS); Bushy Park, 42°43′S, 146°53′E, on *Exocarpus cupressiformis*, 1980, *GK* 31/80.

8. ***Ramalina litorea*** N. Stevens Plate 7, fig. 8.

in *Lichenologist* **18**: 185 (1986). Type: Australia, Queensland, Mackay, Blacks Beach, 1979, *Stevens* 3129NS (MEL! – holotype; evernic acid, lecanoric acid and usnic acid).

Thallus saxicolous, pale yellow-green, small, caespitose, rigid, 0·5–2·0 cm high; branching subdichotomous to irregular, small branchlets or spinules arise laterally from the main branches; branch width 0·2–1·0 mm, subterete to terete or rarely flattened, narrow, apices pointed, fragile; surface shiny to matt, without pseudocyphellae, smooth; holdfast diffuse; soralia absent.

Apothecia common, marginal or lateral below the apices, disc 1·0–2·0 mm diam., plane; margin thin to very thick; spores small, oval or ellipsoid, straight, 8–12 × 4–4·5 μm.

Chemistry. Evernic acid (M), lecanoric acid (t), ± sekikaic acid (t), and usnic acid.

Remarks. Some specimens of *R. litorea* resemble the Hawaiian species *R. microspora* Krempelh. However, the latter species contains divaricatic acid, whereas *R. litorea* contains evernic acid. Herbarium material labelled *R. microspora* from Mauritius and Rodrigues (in the Indian Ocean, 20°S) containing evernic acid and morphologically somewhat similar to the Australian taxon have been treated as *R. litorea* by the author. Further investigation may prove that *R. microspora* comprises two chemical races disjunctly distributed in the Pacific and Indian Oceans.

Distribution and habitat. The full distribution range of *R. litorea* (Fig. 14) is unknown as only five collections have been made in an area from latitudes 14°40′–24°20′S. This saxicolous species has been collected from coastal cliffs, composed of a variety of rock types (granite, siltstone, slates, rhyolitic, breccia, and tuff) indicating it is not substrate specific. Only small colonies grow on the cliff faces, usually at 10–20 m above beach level; although on Lizard Island (14°S, the most northern collection) a specimen was collected at 360 m elevation.

World distribution. Mauritius, Rodrigues Island, and Australia.

Queensland: Lizard I. 14°40′S, 145°28′E, on granite (360 m elev.), 1974, *R. L. Specht* (BRIU3780NS); Cape Hillsborough, 20°56′S, 149°03′E, on rhyolitic breccia (10 m elev.), 1983, *GNS* (BRIU4124NS); Mackay, Blacks Beach, 21°04′S, 149°12′E, on siltstone (10 m elev.), 1979, *GNS* (BRIU3129NS); Great Keppel I, 23°10′S, 150°58′E, substrate unknown, 1976, *U. Allen* (H032240); Double Head, 23°08′S, 150°47′E, on slates (15 m elev.), 1984, *NCS* (BRIU4307NS); Emu Park, 23°15′S, 150°30′E, on slates (10 m elev.), 1984, *NCS* (BRIU4308NS); Agnes Water, 24°20′S, 151°58′E, on rhyolitic agglomerate (5 m elev.) 1984, *NCS* (BRIU4277NS).

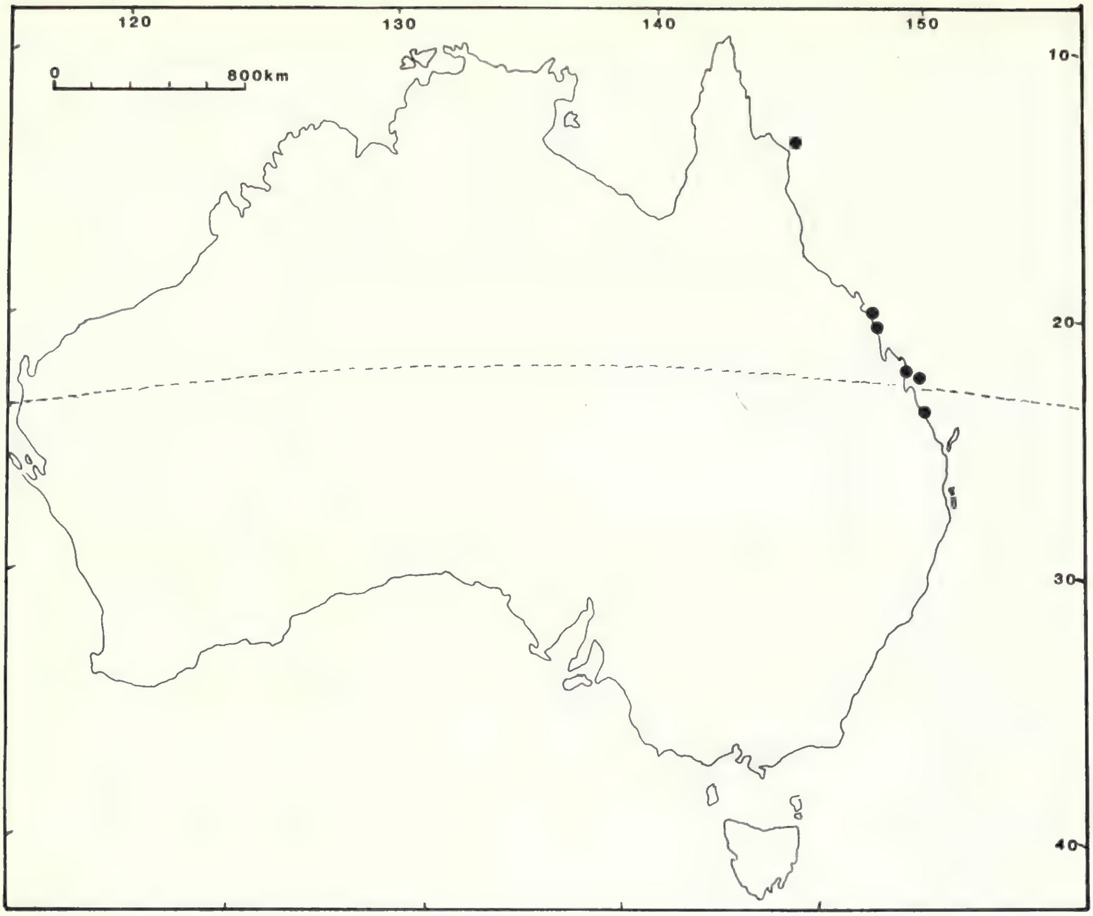

Fig. 14 Distribution of *R. litorea*.

9. ***Ramalina peruviana*** Ach.

Plate 9, figs 1–2.

Lichenogr. Univ.: 599 (1810). Type: South America, Peru, *Lagasta* s.n. (H-ACH! – holotype; BM!, UPS! – isotypes; sekikaic acid aggregate, and usnic acid).

Ramalina farinacea var. *dendroides* Müll. Arg. in *Flora, Jena* **66**: 21 (1883). Type: Australia, New South Wales, Ash Island (Hunter River), 1883, *Ford* s.n. (G! – holotype; sekikaic acid aggregate and usnic acid). Plate 14, fig. 2.

Ramalina farinacea var. *squarrosa* Müll. Arg. in *Flora, Jena* **66**: 21 (1883). Type: Australia, Queensland, Rockhampton, 1883, *Thozet* s.n. (G! – holotype; sekikaic acid aggregate and usnic acid). Plate 14, fig. 1.

Thallus corticolous, pale green to grey-green, tufty, resilient, erect to subpendulous, up to 6·0 cm long; branching subdichotomous to irregular, often intricate with the production of dense fragile branchlets; branch width up to 1·0 mm, branches flat, compressed becoming angularly subterete to terete distally, branches often slightly twisted, apices sharp to blunt, often broken; surface matt, rarely shiny, smooth to rugose, weakly pseudocyphellate either basally or along the entire length; holdfast delimited or diffuse; soralia punctiform, numerous, marginal or lateral, sometimes apical (Plate 1, fig. 2), mounds of soredia often produce small fibrils (Plate 3, fig. 7).

Plate 9 Thallus growth forms in the Australian Ramalinae. Scale in mm. Fig. 1 *R. peruviana* (dense form). Fig. 2 *R. peruviana* (open form). Fig. 3 *R. reducta* (lower surface). Fig. 4 *R. tenella*. Fig. 5 *R. unilateralis* (palmate form). Fig. 6 *R. unilateralis* (large, intricate form). Fig. 7 *R. whinrayi*. Fig. 8 *R. celastri* subsp. *celastri* (narrow form).

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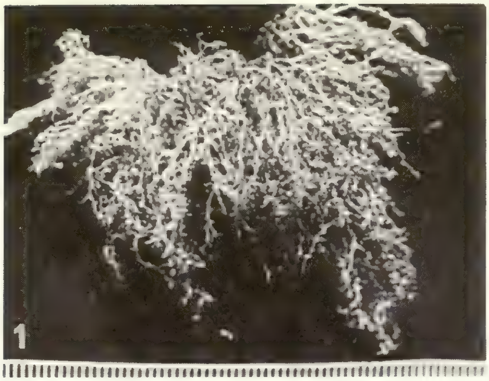
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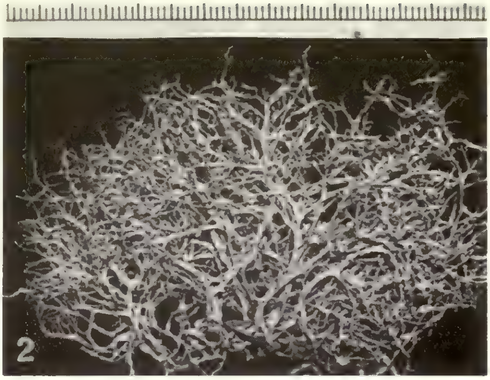
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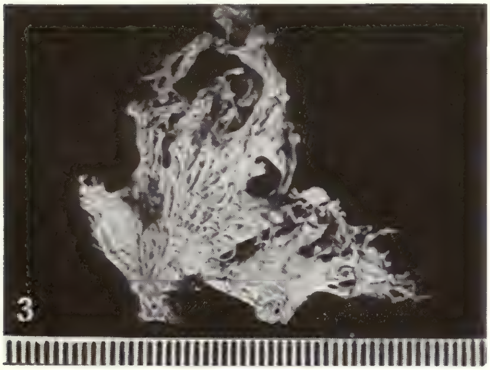
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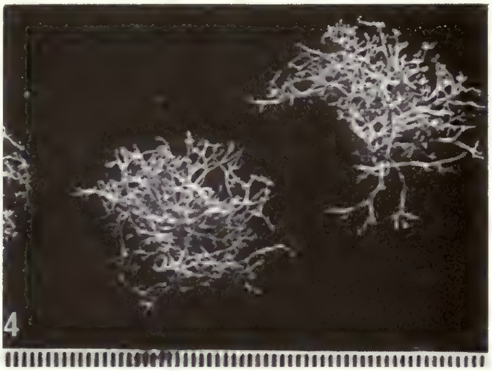
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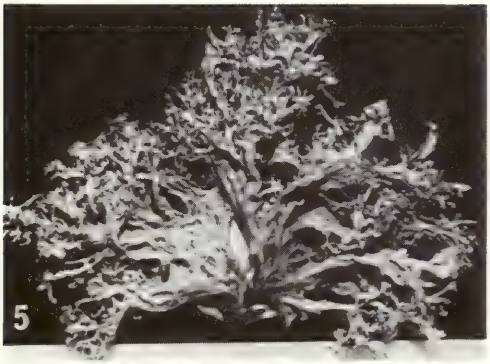
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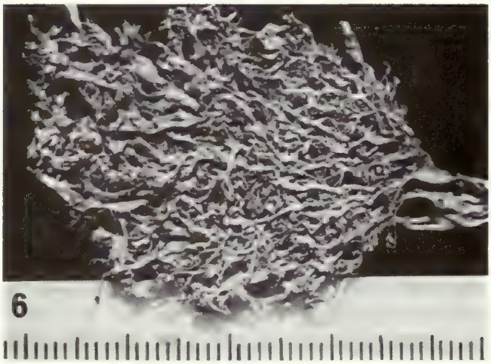
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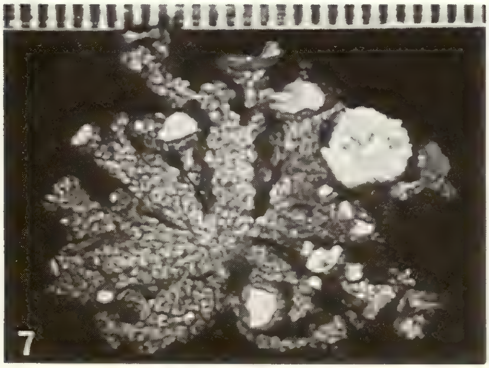
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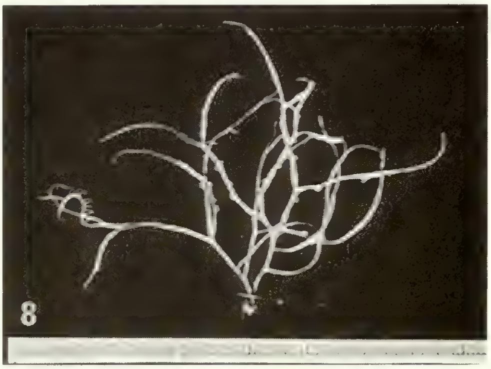
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Apothecia rare, marginal, lateral, disc 2·0 mm diam., concave, margin thick, often crenate; spores narrow, fusiform, straight or rarely curved, 14–16(–18) × 3·5–4·5 μm.

Chemistry. Homosekikaic acid (M), sekikaic acid (M), ramalinolic acid (m/t), 4'-0-demethylsekikaic acid (m/t), 4'-0-methylnorsekikaic acid (m/t), and usnic acid.

Remarks. The holotype material from H and the isotypes material held at BM and UPS are all small pieces and the morphological characters are not well defined, faint pseudocyphellae occur on the basal portion of the branches, and the soralia are not very clear. The Australian material does not closely resemble the morphology of the type material but Krog & Swinscow (1976) commented that some of the East African specimens appeared to differ from the type specimen. When comparing East African material with Australian no differences could be found. *Ramalina peruviana* material examined from Uruguay and Brazil closely resembled Australian specimens and also displayed considerable variation in morphology.

Two previously accepted infra-specific taxa from Australia are reduced to synonymy with *R. peruviana*; these are *R. farinacea* var. *dendroides* and *R. farinacea* var. *squarrosa*, both of which are regarded as ecophenotypes of *R. peruviana*.

Ramalina tenella is the only species in Australia which may be mistaken for *R. peruviana*, but the acid difference sets them apart, the former containing salazinic acid. The Japanese taxon *R. intermediella* Vainio closely resembles the morphology of *R. peruviana* and contains similar acids, but it does not occur in Australia.

Distribution and habitat. Ramalina peruviana is mainly subtropical to warm temperate in distribution (Fig. 15). North of the Tropic of Capricorn it occurs inland at 1000 m elevation at both Atherton Tableland (17°S) and Undara Crater (19°S). Such elevations in the tropics correspond with the reported distribution of the species in the West Indies (17°N) at altitudes between 600–1000 m (Landrón, 1972), and in East Africa (10°N–10°S) between 1000–1800 m (Krog & Swinscow, 1976) allowing for latitudinal adjustment.

Four ecotypes can be distinguished in the Australian taxa although intergradation occurs between each form: (i) the coastal form (which includes *R. farinacea* var. *squarrosa* type material), (ii) a montane form, (iii) a densely branched form found in open-forest habitats in Queensland and (iv) an open sparsely branched form in the open-forest habitats of south-east Queensland and New South Wales (which includes *R. farinacea* var. *dendroides* type material). The differences are shown in Table 10.

Specimens of these four ecotypes were chemically analysed to assess if there was any correlation between their chemistry and the morphological differences. None was found, but variation in the quantity of some of the minor metabolites was obvious. This variation could be correlated with inland and coastal locations, i.e. coastal specimens had only trace amounts of 4'-0-methylnorsekikaic acid, but specimens from inland sites contained noticeably more.

Jørgensen (1977) commented that *R. peruviana* may need to be subdivided because of the number of morphotypes present, but from the survey of Australian material it is felt that any subdivision is unwarranted because of the intergradation between ecotypes.

All collections in Australia have been corticolous. The main phorophytes for the coastal ecotype are the mangroves *Ceriops tagal* and *Rhizophora stylosa*. Once these species reach their distribution limit at 28°S, *R. peruviana* is found on various coastal trees. In the mountains this taxon occurs on several rain-forest tree species and in the open-forest habitat, shrubs such as *Lantana* are the host. This taxon is not substrate specific; in South America it has been found on fence posts (Osorio, in litt.).

World distribution. Africa, Australia, New Zealand, several Pacific Islands, South America, and Tristan da Cunha.

Queensland: Atherton, 5 km N of, 17°14′S, 145°29′E, 1970, *E. Dahl* (0); Atherton, 2 km SE of, 17°16′S, 145°30′E, on *Casuarina* sp., 1983, *HS* (CBG8302451); Undara Crater, 18°23′S, 144°43′E, on rain-forest tree, 1977, *NCS* (BRIU3546NS); Forty Mile Scrub, 18°03′S, 144°53′E, on rain-forest tree, 1983, *GNS* (BRIU4115NS); St Lawrence, 22°20′S, 149°32′E, on *Ceriops tagal*, 1978, *NCS* (BRIU2678NS); Gladstone, South Trees Inlet, 23°52′S, 151°19′E on *Ceriops tagal*, 1980, *GNS* (BRIU3592NS); Tannum Sands,

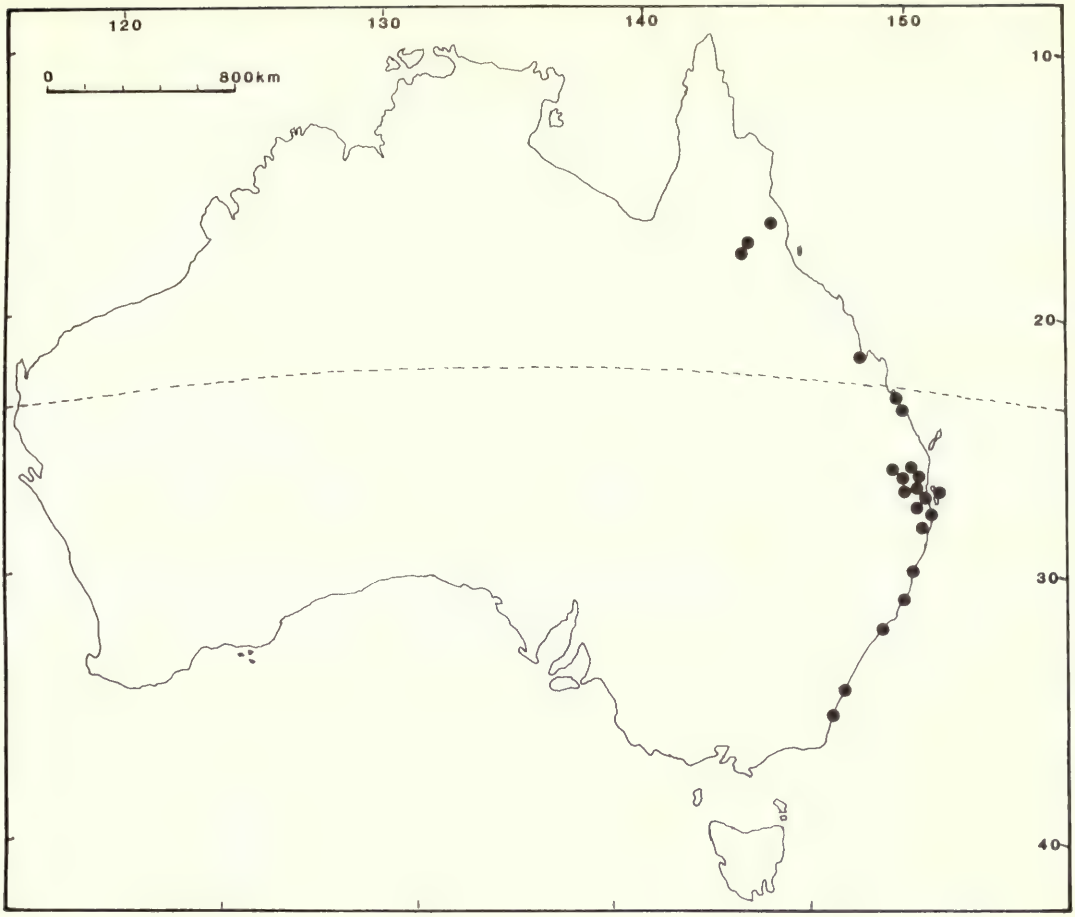

Fig. 15 Distribution of *R. peruviana*.

23°58′S, 151°23′E, on *Rhizophora stylosa*, 1975, *RWR* (BRIU876RR); Turkey, 24°06′S, 151°38′E, on *Ceriops tagal*, 1975, *GNS* (BRIU1154NS): Jimna, 26°40′S, 152°28′E, on *Araucaria cunninghamii*, 1980, *RWR* (BRIU2197RR); Maleny, 26°46′S, 152°51′E, on dead tree, 1982, *GNS* (BRIU3708NS); Bunya Mts, 26°50′S, 151°40′E, on shrubs, 1979, *GNS* (BRIU2971NS); Mt Mee, 27°05′S, 152°42′E, on *Flindersia* sp., 1979, *GNS* (BRIU3324NS); Mt Byron, W of 27°06′S, 152°37′E, on *Araucaria cunninghamii* 1982, *GNS* (BRIU3624NS); Brisbane, Serpentine Ck, 27°22′S, 153°08′E, on *Ceriops tagal,* 1975, *GNS* (BRIU1097NS); Stradbroke I. Amity Pt, 27°24′S, 153°25′E, on *Lumnitzera racemosa*, 1977, *GNS* (BRIU2050NS); Brookfield, 27°30′S, 152°55′E, on *Citriobatus pauciflora*, 1983, *GNS* (BRIU3694NS); St Lucia, 27°30′S, 153°00′E, on *Bauhinia alba*, 1976, *GNS* (BRIU3322NS); Worlds End Pocket, 27°31′S, 152°45′E, on *Mallotus celaoxyloides*, 1983, *P. Forster* (BRIU3705NS); Pt Talburpin, 27°39′S, 153°18′E, on *Avicennia marina*, 1980, *GNS* (BRIU3548NS); Little Rocky Pt, 27°43′S, 153°21′E, on *Ceriops tagal*, 1977, *GNS* (BRIU480NS); Stradbroke I. south point, 27°44′S, 153°25′E, on mangrove, 1975, *H. T. Clifford* (BRIU3074RR); Cunninghams Gap, 28°03′S, 152°24′E, on rain-forest tree, 1975, *NCS* (BRIU3695NS); Binna Burra, 28°12′S, 153°11′E, on rain-forest tree, 1976, *GNS* (BRIU3693NS); O'Reillys, 10 km N of, 28°13′S, 153°06′E, on Gympie tree, 1983, *GNS* (BRIU3724NS). **New South Wales**: Wilsons Ck, 28°34′S, 153°27′E, on rain-forest tree, 1980, *GNS* (BRIU3320NS); Goonengarry, 28°37′S, 153°28′E, on *Citriobatus pauciflora*, 1980, *GNS* (BRIU3319NS); The Channons, 28°39′S, 153°16′E, on *Lantana*, 1982, *GNS* (BRIU3526NS); Lismore, 28°48′S, 153°16′E, on *Acacia* sp., 1976, *R. Moodie* (BRIU2855NS); Nambucca, 12 km SSW. of, 30°41′S, 153°00′E, on *Avicennia marina*, 1982, *GNS* (BRIU3670NS); Taree, Saltwater, 31°54′S, 152°34′E, on tree, 1977, *JAE* (JAE 3999); Hunter R. Ash I. 32°56′S, 151°46′E, 1883, *E. Forde* (G); Broulee, 35°52′S, 150°09′E, on shrubs, 1970, *JAE* (JAE 128); Wagonga Inlet, 36°12′S, 150°08′E, 1908, *G. H. Halligan* NSW L4304).

Table 10 Comparison of morphological characters found in four ecotypes of *Ramalina peruviana*.

Character	Morphotype A	Morphotype B	Morphotype C	Morphotype D
Type of branching	dense, irregular distally intricate	open, subdichotomous to irregular	open, subdichotomous	dense, irregular
Shape of branches	compressed, flat to subterete	compressed, flat to subterete	subterete to terete	compressed, flat to subterete
Width of branches	0·2–0·5 mm	0·5–1·0 mm		0·2–0·5 mm
Shape of apices	hooked or broken off	attenuate, some broken off	attenuate, some broken off	hooked or broken off
Pseudocyphellae	distinct to indistinct along entire length		absent or indistinct	distinct in basal region of branch
Soralia	marginal and lateral punctiform, large	marginal punctiform, medium to large	lateral, small punctiform or slightly 'farinacea-like'	marginal, punctiform small
Soredia	dense, forming mounds which produce fibrils	small extrusion on the surface	not raised above level of surface	dense, forming mounds
Habitat	dry, remanent rainforest or isolated trees, open sites	open forest in full sun	montane rainforest shady sites	coastal mangroves in full sun

10. ***Ramalina reducta*** Krog & Swinscow Plate 9, fig. 3.

in *Norw. J. Bot.* **23**: 172 (1976). Type: Ethiopia, Bale Province, Dinshu, *Tapper* 933 (BM! – holotype; O! – isotype; psoromic acid and usnic acid).

Thallus corticolous, grey-green or pale green, erect, flaccid, up to 4 cm long; branching sparse, initially a palmate lobe producing several multi-divided lacinae; branch width 10 mm at base, separate lacinae to 5 mm, branches compressed, flat, apices tattered or capillaceous; surface matt, rugose, often cracking; a continuous lower cortex lacking with the medulla overlaid by cartilaginous strands forming a reticular pattern, some strands becoming detached at one end; holdfast delimited; soredia pale green, produced from the exposed medulla.

Apothecia rare, marginal, disc to 2·5 mm diam, concave to plane, margin entire; spores few, ellipsoid, curved, 13–18 × 4–5(–6) μm.

Chemistry. Psoromic acid and usnic acid.

Remarks. The Australian specimens are much larger than those examined from East and South Africa and cannot be regarded as 'inconspicuous' as described by Krog & Swinscow (1976). This species is easily recognised by the anastomosing strands of cartilaginous hyphae on the exposed lower surface. The production of psoromic acid distinguishes it from any other Ramalinae in Australia.

Distribution and habitat. This taxon has a restricted distribution range (Fig. 16). It occurs in the open-forest uplands of the New England Plateau, a granitic/basaltic tableland rising to over

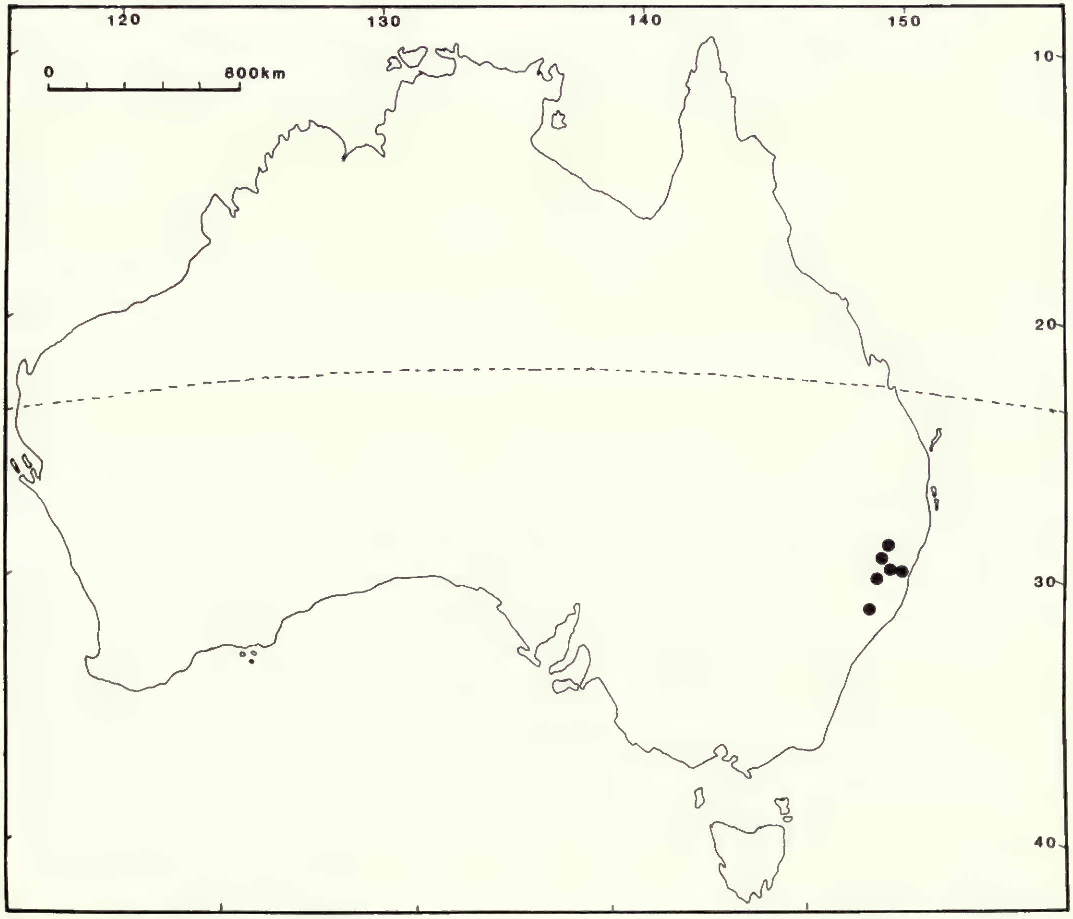

Fig. 16 Distribution of *R. reducta*.

1300 m in the subtropics. The narrow ranges of latitude and longitude in *R. reducta* distribution coincide with a 12°C mean maximum annual temperature isotherm. The distribution area experiences wet summers and drier winters, indicating that the summer may be the growing period for this species. This particular set of environmental factors is not found in other areas.

To the north only individual peaks reach an elevation of over 1300 m and these are covered in rain-forest; and to the south, where the Australian Alps attain a height of over 2000 m, the rainfall is either uniform throughout the year or occurs during the winter. Seasonality may be a factor which inhibits the occurrence of *R. reducta* further south.

Krog & Swinscow (1976) recorded East African material from the upper montane forests between 2600 m and 3100 m altitude, which when adjusted for latitude is comparable with the occurrence of *R. reducta* in Australia.

Ramalina reducta was collected from *Acacia, Casuarina,* and *Banksia* spp. growing in well lit open-forest communities. A large monospecific community of this taxon was found at Ebor Falls, New South Wales, growing on all three phorophytes, in an area exposed to spray from the falls under certain wind conditions. In this environment thalli reached 4 cm in length and many produced apothecia, indicating that such a habitat promoted optimal growth. No fertile thalli were reported from the East African material.

World distribution. Africa and Australia.

New South Wales: Glen Innes, 12 km E of, 29°42′S, 151°50′E, on *Acacia parvipinula*, 1983, *GNS* (BRIU3782NS); Ben Lomond, 30°00′S, 151°42′E, on dead *Acacia* sp., 1980, *GNS* (BRIU3237NS); 1976, *JAE* (JAE 2435); Coutts Water, Ebor-Dorrigo Rd, 30°22′S, 152°30′E, on shrubs, 1982, *GNS* (BRIU3633NS); Ebor Falls, 30°25′S, 152°20′E, on *Banksia* sp., 1982, *GNS* (BRIU3632NS); on *Acacia* sp., 1982, *GNS* (BRIU3698NS); on *Casuarina* sp., 1982, *GNS* (BRIU3699NS); Walcha Road, 30°59′S, 151°30′E, on *Acacia* sp., 1982, *GNS* (BRIU3700NS); Topdale, 25 km E of Nundle, 31°30′S, 151°25′E, on *Acacia* sp., 1984, *NCS* (BRIU4297NS); Glenbawn Dam, 32°05′S, 151°00′E, on *Acacia* sp., 1981, *AA* (BRIU3611NS).

11. ***Ramalina tenella*** Müll. Arg. Plate 9, fig. 4

in *Flora, Jena* **62**: 162 (1879). Type: Brazil, São Paulo, Apiahy, 1877, *Puiggari* 152 (G! – holotype; salazinic acid, protocetraric acid (trace), three unknowns, usnic acid).

Thallus corticolous, pale green to yellow-green, erect, rigid, delicate, up to 3·0 cm high; branching subdichotomous with short lateral branches sometimes producing numerous distal branchlets; branch width to 1·0 mm, flat basally thereafter subterete; surface matt; short, linear pseudocyphellae; holdfast delimited; soralia apical and lateral on main branches and apical on secondary branches.

Apothecia unknown.

Chemistry. Salazinic acid ± protocetraric acid, three unknowns, and usnic acid.

Remarks. This taxon has a distinctive growth form when the branching is sparse; when densely branched it resembles *R. peruviana*. The presence of salazinic acid sets it apart from the sekikaic acid taxon *R. peruviana*. Krog & Swinscow (1976) stated that *R. tenella* resembled *R. dendriscoides* Nyl., a species which does not occur in Australia, although some early collections of *R. peruviana* were given the name *R. dendriscoides* (Appendix 1).

Distribution and habitat. Ramalina tenella occurs in isolated, high rainfall pockets along the Queensland coast between 16°S and 24°S (Fig. 17). Uncommon in occurrence, it grows profusely in the areas it inhabits. Material collected from the more northern latitudes always contained three unknown compounds which did not occur in the material from latitudes 21°S–24°S. Lack of bulk material of this species prevented the identification of the unknowns by chemical analysis. Specimens lacking the unknowns were usually found to produce lateral soralia in addition to apical soralia, in contrast to the more northern collections which rarely produced lateral soralia.

Ramalina tenella grows on the twigs of *Ceriops tagal* and *Rhizophora stylosa* in sheltered but well-lit habitats within the mangrove community. It is found in association with *R. subfraxinea*

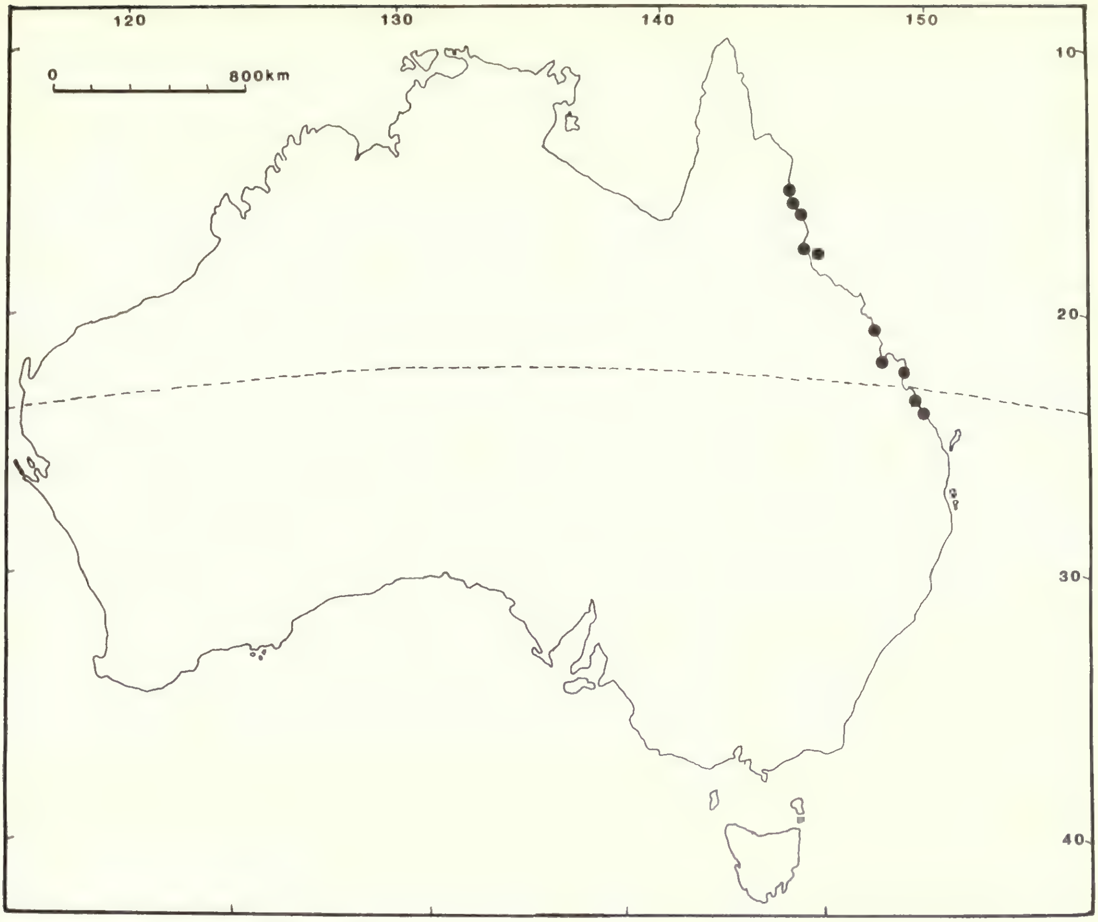

Fig. 17 Distribution of *R. tenella*.

var. *confirmata, R. pacifica, R. exiguella, R. nervulosa* var. *nervulosa*, and *R. nervulosa* var. *luciae*.

World distribution. Africa, Australia, New Hebrides, and South America.

Queensland: Daintree R, 16°15′S, 145°21′E, on *Ceriops tagal*, 1975, *D. Tarte* (BRIU2253NS); Mossman, Saltwater Ck, 16°25′S, 145°25′E, on *Ceriops tagal*, 1983, *C. McCracken* (BRIU4300NS); Mossman, Rifle Club, 16°28′S, 145°25′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4127NS); Cairns, 16°45′S, 145°45′E, 1974, *D. Tarte* (BRIU2470NS); Murray R, 18°05′, 146°01′E, on *Ceriops tagal*, 1978, *D. Tarte* (BRIU3122NS); Hinchinbrook I, 18°20′S, 146°15′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3134NS); Eimeo, 21°09′S, 149°10′E, on *Ceriops tagal*, 1977, *GNS* (BRIU2791NS); on *Rhizophora stylosa*, 1976, *GNS* (BRIU2469NS); Corio Bay, 23°00′S, 150°45′E, on *Ceriops tagal*, 1975, *D. Tarte* (BRIU1172NS); Gladstone, Wiggins Ck, 23°50′S, 151°15′E, on *Ceriops tagal*, 1980, *GNS* (BRIU3549NS); Turkey, 24°06′S, 151°38′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1282NS).

12. ***Ramalina unilateralis*** F. Wilson Plate 9, figs 5–6.

in *Victorian Nat.* **6**: 69 (1889). Type: Australia, Victoria, Warrnambool, *F. R. M. Wilson* 432 (G! – lectotype herein designated; divaricatic acid and usnic acid).

Thallus corticolous, pale green, caespitose to subpendulous, up to 4 cm long, exceptionally to 7 cm; branching irregular, dense; branch width 1–3 mm, flat to subterete, sometimes palmate at the base to 8 mm broad, distally producing numerous fine lacinae; surface cartilaginous, smooth and shiny, rarely matt; holdfast delimited; soralia occur in eroded patches at intervals along the lower surface where the branches have split and flattened out (Plate 1, fig. 6) and also at the apices.

Apothecia rare, disc 2·0 mm diam., concave to plane; margin entire; spores ellipsoidal, straight or rarely curved, 10–12 × 4–4·5 μm.

Chemistry. Divaricatic acid and usnic acid.

Remarks. The specimens held at G are regarded as the lectotype of *R. unilateralis* as no other Wilson material appears to exist. It is thought that the type may have been lost with numerous other Wilson types in 1907 (Filson, 1976).

The morphology of some *R. pollinaria* specimens resembles the morphology of this taxon, and it was this name that was given to *R. unilateralis* specimens by early lichenologists. However, *R. pollinaria* contains evernic acid, whereas *R. unilateralis* contains divaricatic acid.

Some specimens of *R. canariensis* resemble *R. unilateralis*; however, the texture of the surface is different. Reduced growth forms of the latter taxon may be mistaken for *R. fimbriata*, but this species is saxicolous in Australia whereas *R. unilateralis* is corticolous and generally much larger in size. All three species contain divaricatic acid.

Distribution and habitat. Collections of this cool temperate species in Australia have been made from sea-level to elevations of up to 1150 m (Fig. 18). Although corticolous in Australia *R. unilateralis* becomes saxicolous at colder latitudes, e.g. Macquarie I. (55°S) and Tierra del Fuego (54°S). It appears to tolerate a broad range of environments. The type material was collected at

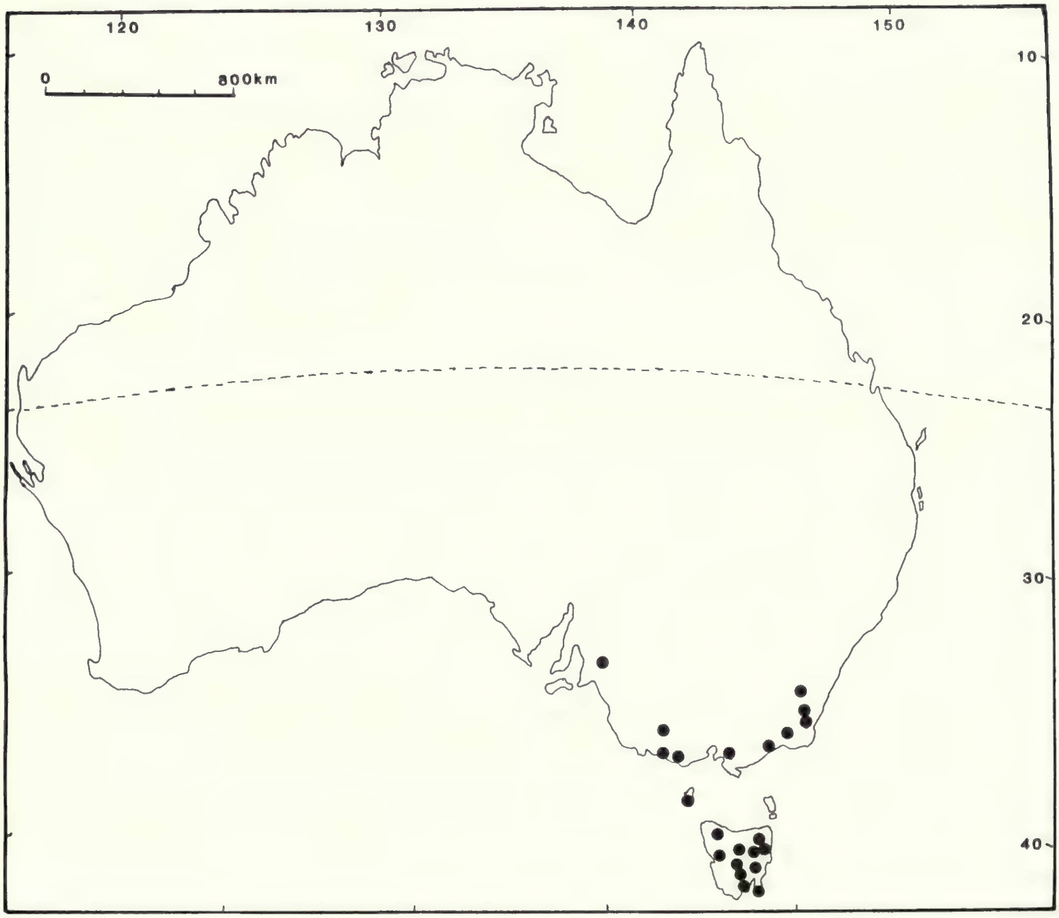

Fig. 18 Distribution of *R. unilateralis*.

sea-level, and other coastal sites are Lakes Entrance, Westernport Bay, and Portland; inland collections above 1000 m were at Nimmitabel, New South Wales, and Old Man's Head, Tasmania. Material cited from South Africa was collected at elevations of 2000 m at latitude 34°S, and from Chile, latitude 53°30′S at an elevation of 800 m.

World distribution. South Africa, Australia, and South America.

New South Wales: Nimmitabel, 36°31′S, 149°17′E, on *Banksia* sp., 1976, *JAE* (JAE 1623); Nimmitabel, 36°31′S, 149°15′E, on *Prunus*. 1980, *GNS* (BRIU3781NS). **Australian Capital Territory**: Mt Coree, 35°20′S, 148°50′E, on tree, 1970, *E. Dahl* (0). **Victoria**: Bonang, 17 km N of, 37°03′S, 148°49′E, on *Acacia* sp., 1978, *D. Verdon* (CBG7811003); Billywing Forest, 37°10′S, 142°30′E, on *Acacia baileyi*, 1981, *RWR* (BRIU2451RR); Spring Ck Gap, 37°15′S, 148°30′E, on *Acacia* sp., 1978, *JAE* (JAE 5137); Metung, 37°53′S, 147°51′E, on tree, 1889, *F. R. M. Wilson* (MEL 9420); Upper Maffra, 37°54′S, 146°51′E, on conglomerate, 1886, *F. R. M. Wilson* (NSW L4312); Hastings 5 km N of, 38°18′S, 145°11′E, on *Avicennia marina*, 1975, *RWR* (BRIU973RR); Warrnambool, 38°23′S, 142°20′E, 1886, *F. R. M. Wilson* (NSW L4311); Curdies Ck, 38°25′S, 143°00′E, on bush, 1885, *F. R. M. Wilson* (NSW L4315). **South Australia**: Springton 6·5 km W of, 34°43′S, 139°05′E, on *Hakea* sp., 1976 *JAE* (JAE 2261); Mt Barker, 35°06′S, 138°51′E, on dead twig, 1981, *RWR* (BRIU2427RR). **Tasmania**: Trowutta, 41°02′S, 145°05′E, on *Pyrrhus* sp., 1981, *GK* 391/81; Mt Barrow Chalet, 41°22′S, 147°27′E, on *Acacia dealbata*, 1969, *GB & JC* (H032547); Upper Esk, 41°26′S, 147°44′E, on *Acacia dealbata*, 1981, *GK* 60/81; Cressy, 41°43′S, 147°02′E, on dead *Acacia*, 1964, *JC* (H032561); Central Plateau, 41°45′S, 146°50′E, on *Athrotaxis cupressoides*, 1980, *GK* 508/80; Friendly Beach, 42°00′S, 145°15′E, on *Acacia* sp., 1968, *GB & JC* (H032332); Shannon Lagoon, 42°08′S, 146°51′E, on dead eucalypt, 1980, *GK* 153/80; Lake Crescent, 42°10′S, 147°09′E, on dead Acacia, 1969, *GB* (H032544); Old Mans Head, 42°12′S, 147°13′E, on dead *Acacia*, 1964, *GB & JC* (H032333); Ouse, 29 km N of, 42°14′S, 146°44′E, on *Acacia* sp., 1964, *GB & JC* (H032557); Dee, 6 km E of, 42°17′S, 146°38′E, on *Acacia* sp., 1970, *GB* (H032548); Tarraleah, 42°18′S, 146°26′E, on *Acacia dealbata*, 1980, *GK* 346/80; Ellendale, 42°38′S, 146°43′E, on old oak, 1980, *GNS* (BRIU3231NS); Sorrel-Nugent Rd, 42°46′S, 147°39′E, on briar and *Acacia* sp., 1964, *GB* (H032330); Cygnet, Bradleys Property, 43°09′S, 147°05′E, on dead willow, 1973, *GB* (H032322); Port Arthur, 43°13′S, 147°50′E, 1908, *Mrs Townsend* (NSW L4318).

13. *Ramalina whinrayi* [‘*whinrayii*’] N. Stevens Plate 9, fig. 7.

in *Lichenologist* **18**: 187 (1986). Type: Australia, Hogans Island (Bass Strait), 1973, *Whinray* s.n. (MEL! – holotype; divaricatic acid ± nordivaricatic acid).

Thallus saxicolous, grey-green, caespitose, rigid, up to 1·0 cm high, branching sparse; branches arising from the base, branch width 1·0–2·5 mm, subterete to terete, rarely flattened, apices attenuate or blunt; surface matt; pseudocyphellae coarse, large, punctiform, numerous; holdfast delimited or diffuse when in colonies; soralia absent.

Apothecia numerous, disc 3–10 mm diam., concave becoming plane to convex, terminal and lateral, or at the axils of bifurcating branches, spores ellipsoid, straight 12 × 4·5–5·0 μm.

Chemistry. Divaricatic acid ± nordivaricatic acid or sekikaic acid 4’-0-demethylsekikaic acid and usnic acid.

Remarks. The anatomy of *R. whinrayi* differs from that of any of the other Australian taxa, but it is similar to the anatomy of *R. capitata* (= *R. strepsilis*) from the northern hemisphere.

Distribution and habitat. Ramalina whinrayi is restricted in distribution to some of the Bass Strait islands and one site on the Tasmanian north coast (Fig. 19). This saxicolous taxon grows on granitic boulders at altitudes from 36–84 m above sea-level. The islands where this taxon occurs lie along a southeast line – from the Hogan Group, the Kents Group to Craggy Island between latitudes 39°12′S and 40°45′S. *Ramalina whinrayi* also occurs at The Nut, Stanley, Tasmania, where it occurs in overhangs on a basaltic cliff facing the ocean and exposed to strong winds.

World distribution. Australia.

Bass Strait: Hogans Group: Long Islet, 39°12′S, 147°00′E, on granite, 1973, *JW* (MEL1012965); Hogans I, 39°13′S, 146°59′E, on granite, 1973, *JW* (MEL1012948) Type; **Kents Group**: North East I, 39°27′S,

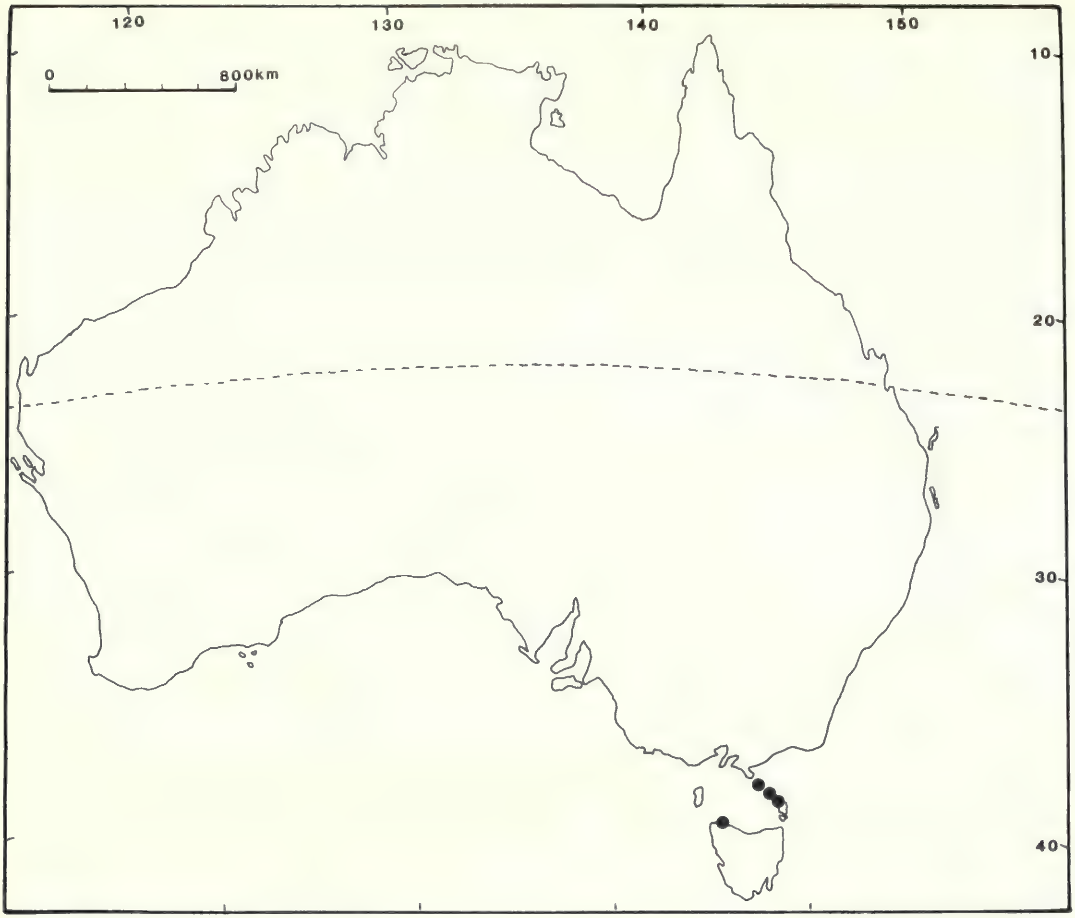

Fig. 19 Distribution of *R. whinrayi*.

147°25′E, on granite, 1971, *JW* (MEL1012636); Craggy I, 39°41′S, 147°40′E, on granite, 1972, *JW* (MEL1013031). **Tasmania**: The Nut, near Stanley, 40°45′S, 145°18′E, on basalt, 1973, *GB* (H032796).

14. ***Ramalina celastri*** (Sprengel) Krog & Swinscow

in *Norw. J. Bot.* **23**: 159 (1976).

Parmelia celastri Sprengel, *Syst. Veget.* **4** (2): 328 (1827). Type: Cap. B. Spei, *Eklon* (S! – holotype; FH! – isotype; usnic acid).

subsp. ***celastri*** Plate 9, fig. 8; Plate 10, fig. 1; Plate 15, fig. 4.

Ramalina fraxinea β *yemensis* Ach., *Lichenogr. Univ.*: 602 (1810). Type: Arabia, *Forskål*, herb. Acharius (H! – holotype). – *Ramalina yemensis* (Ach.) Nyl. in *Bull. Soc. Linn. Normandie* II, **4**: 144 (1870).
Ramalina ecklonii auct., non Sprengel.

Thallus corticolous, rarely saxicolous, pale green to grey-green, erect, subpendulous to pendulous, up to 12 cm long, exceptionally to 30 cm; branching initially trichotomous, either

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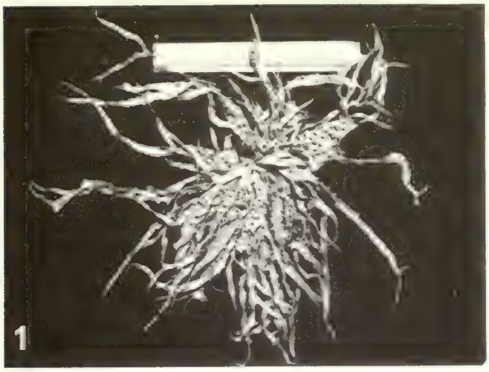
Plate 10 Thallus growth forms in the Australian Ramalinae. Scale in mm. Fig. 1 *R. celastri* subsp. *celastri* (common form). Fig. 2 *R. celastri* subsp. *ovalis* (broadest form). Fig. 3 *R. inflata* subsp. *perpusilla* (coastal ecotype). Fig. 4 *R. inflata* subsp. *perpusilla* (inland ecotypes). Fig. 5 *R. inflata* subsp. *inflata* (open-forest ecotype). Fig. 6 *R. inflata* subsp. *inflata* (closed-forest ecotype). Fig. 7 *R. inflata* subsp. *australis*: LHS divaricatic acid specimen RHS sekikaic acid specimen. Fig. 8 *R. fissa* (branch at centre top of photo shows medulla due to splitting apart).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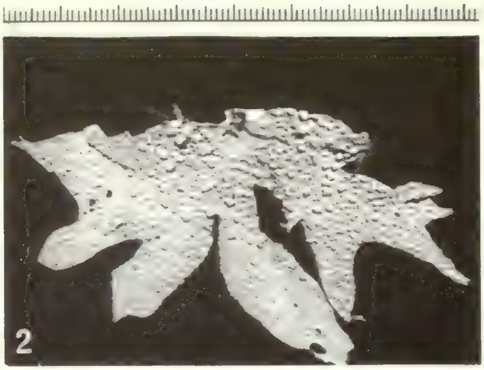
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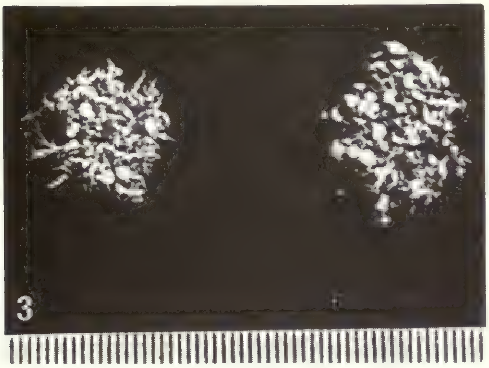
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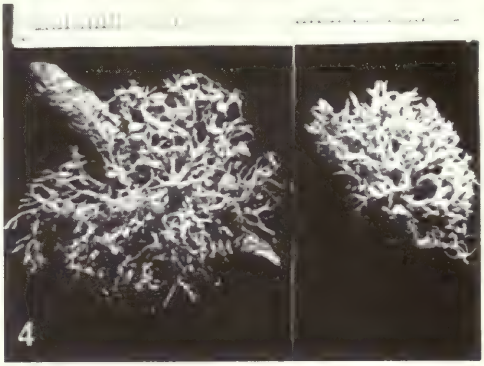
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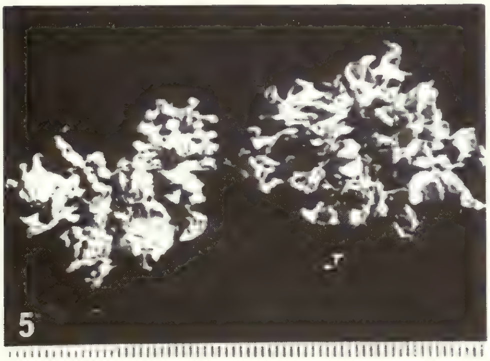
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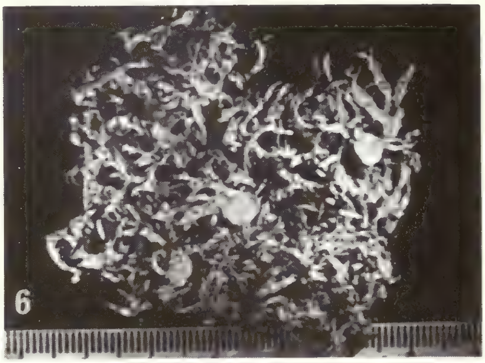
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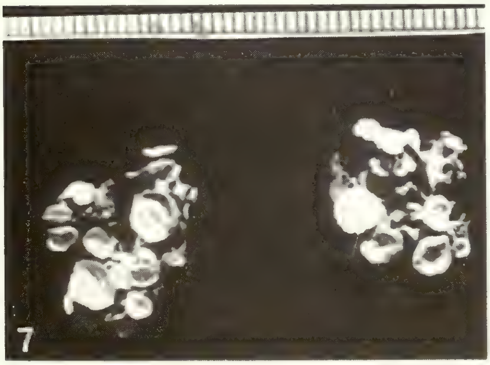
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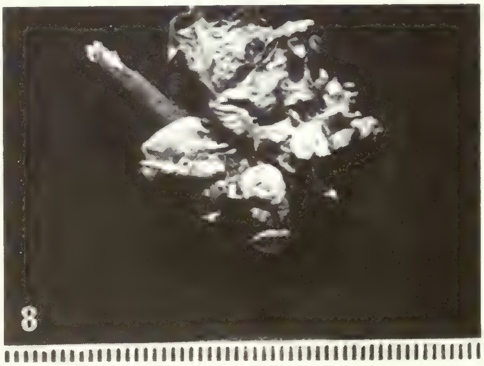
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remaining as a three-lobed thallus or thereafter dividing subdichotomously or irregularly, often producing densely branched thalli, rarely producing small branchlets at right angles to the primary branches; branch width (1–)2–5 mm exceptionally to 20 mm, branches compressed ranging from narrow and canaliculate with apices attenuate to broad and flat with apices acute or blunt; surface matt, smooth to rugose, membraneous or coarse and ridged with strands of chondroid tissue, cracks or holes may appear between these strands; pseudocyphellae usually present; holdfast delimited; soralia absent.

Apothecia numerous, marginal on narrow branches, laminal and marginal on broader branches; apothecia occasionally appear on both upper and lower surfaces of the branch; disc 0·5–2·0 mm diam., plane to convex; margin narrow, entire, smooth or crennate, almost disappearing at maturity; spores oval, ellipsoid to slightly fusiform, mainly straight to slightly curved, (10–)12–16 × 4–6 μm.

Chemistry. Usnic acid only.

Remarks. The name *R. ecklonii* (Sprengel) Meyen & Flotow was incorrectly applied to this species for a long time. Krog & Swinscow (1976) rejected the name *R. ecklonii*, applying Article 69 of the Code, and chose *R. sprengelii* as a nomen novum for it. Material collected by Ecklon from Cape of Good Hope was cited as the holotype. This material is very small, whereas an isotype held at FH in Tuckerman herbarium comprises a number of thalli in good condition. All of these specimens are narrow and canaliculate in form. Comparison of the type material with the narrow ecotype found in Australia showed them to be morphologically similar.

Specimens bearing this narrow morphology are often confused with *R. linearis* Swartz, but there are distinct differences which easily separate the two (Stevens, 1983*b*). Broad thalli which belong to *R. celastri* subsp. *celastri* resemble the morphology of the holotype of *R. yemensis* (Ach.) Nyl. (*R. fraxinea* β *yemensis* Ach.). This variability in the width of branches caused many new taxa to be described, some of which Hue (1890: 265) listed as synonyms of *R. yemensis*.

Weber & Wetmore (1963, 1972) listed the names *R. ecklonii* Sprengel, *R. ecklonii* var. *membranacea* (Laurer) Müll. Arg., *R. ecklonii* var. *tenuissima* Meyen & Flotow, *R. linearis* Sw., and *R. yemensis* (Ach.) Nyl. as occurring in Australia, but examination of these specimens has identified them as belonging to *R. celastri* subsp. *celastri*.

Examination of some South American material indicates several of these species may be morphotypes of *R. celastri* subsp. *celastri*. *R. ecklonii* var. *lobulifera* Malme closely resembles the broad morphotype found in Australia. Other species, e.g. *R. laevigata* and *R. continentalis*, appear to be morphotypes of *R. celastri* subsp. *celastri*, but more research into the South American taxa is necessary before taxonomic conclusions can be established. The position of *R. cumanensis* Fée in this group of taxa has yet to be determined; narrow canaliculate morphotypes in Australia have been found which closely resemble it. Krog & Swinscow (1976) commented that a specimen of *R. celastri* from Mt Kenya resembled *R. cumanensis*, and Landrón (1972) was convinced that *R. cumanensis* and *R. ecklonii* were the same species and reduced the latter name to synonomy. This problem is still to be resolved.

Distribution and habitat. Ramalina celastri subsp. *celastri* morphotypes extend from the subtropics (26°S) to the temperate region (38°S) (Fig. 20), with the coastal occurrence more restricted in latitude (28°S to 35°S). The inland distribution is extensive in eastern Australia, occurring up to 200 km from the coast. It also has a wide altitudinal range, extending from sea-level to the mountains.

Narrow canaliculate morphs occur in montane forest habitats on a variety on tree species. In these habitats the rainfall usually exceeds 1500 mm per annum and mists are common throughout the year. Broad, flat thalli (some reaching widths of over 10 mm) occur in the drier open-forest areas on several phorophytes, species of *Acacia* being the most common, e.g. *A. leiocalyx, A. concurrens, A. irrorata, A. orites, A. melanoxylon,* and *A. mearnsi*. The lichen also occurs on *Alphitonia excelsior* and on the thorny shrubs *Citriobatus pauciflora* and *Capparis arborea*.

Ramalina celastri subsp. *celastri* is usually found growing in association with the fistulose taxa

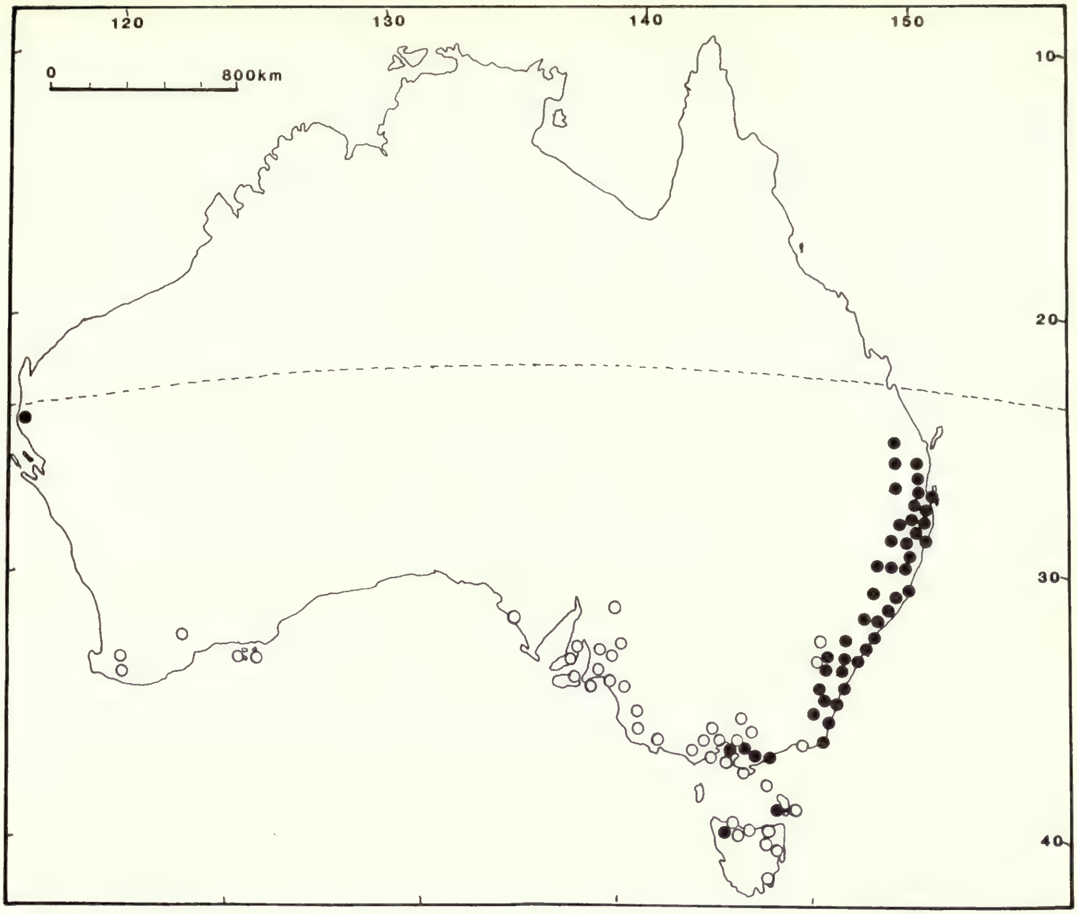


Fig. 20 Distribution of *R. celastri* subsp. *celastri* ● and subsp. *ovalis* ○.

R. inflata subsp. *perpusilla* and *R. inflata* subsp. *inflata* up to 1000 m, and with *R. reducta* at altitudes above 1300 m.

World distribution. Pan-subtropical.

Queensland: Narayen, 25°48′S, 151°10′E, on scrub tree, 1980, *N. Gibson* (BRIU3287NS); Kingaroy, 3 km SW of, 26°34′S, 151°48′E, on dead shrub, 1979, *HS* (CBG8000062); Jimna, 26°40′S, 152°28′E, on *Acacia* sp., 1980, *GNS* (BRIU3354NS); Bunya Mts, 26°50′S, 151°40′E, on *Acacia* sp., 1979, *GNS* (BRIU3289NS); Mt Mee, 27°06′S, 152°42′E, on *Citriobatus pauciflora*, 1971, *RWR* (BRIU1919RR); Maclagan, 27°10′S, 151°38′E, on *Acacia* sp., 1979, *GNS* (BRIU3290NS); Toowoomba, Highfields, 27°23′S, 151°58′E, on *Alphitonia* sp., 1983, *GNS* (BRIU4066NS); Rosewood, 27°39′S, 152°36′E, on *Alphitonia* sp., 1982, *GNS* (BRIU3559NS); Pittsworth, 20 km W of, 27°45′S, 151°27′E, on *Carissa ovata*, 1983, *M. Olsen*, (BRIU3761NS); Tamborine Mt 27°55′S, 153°12′E, on shrub, 1979, *GNS* (BRIU3012NS); Mt Cordeaux, 28°03′S, 152°23′E, on rainforest tree, 1978, *GNS* (BRIU3099NS); Warwick, Apex Park, 28°13′S, 152°02′E, on oak tree, 1980, *GNS* (BRIU3235NS); Binna Burra, 28°12′S, 153°11′E, on *Acacia* sp., 1979, *RWR* (BRIU2153RR); O'Reillys, 28°15′S, 153°08′E, on *Eugenia* sp., 1983, *GNS* (BRIU3735NS); Springbrook, 28°14′S, 153°16′E, on *Acacia orrites*, 1983, *GNS* (BRIU3759NS); Wilsons Peak, 28°15′S, 152°30′E, on *Acacia* sp., 1978, *GNS* (BRIU3829A.NS); Kelvin Falls, 28°27′S, 152°06′E, on *Casuarina* sp., 1980, *NCS* (BRIU3286NS). **New South Wales**: Undercliff Falls, 28°38′S, 152°10′E, on *Acacia melanoxylon*, 1981, *GNS* (BRIU3652NS); Lismore, 28°48′S, 153°16′E, on *Acacia* sp., 1976, *R. Moodie* (BRIU2850NS); Yamba, 29°27′S, 153°20′E, on *Avicennia marina*, 1977, *GNS* (BRIU2124A.NS); Glen Innes, 35 km S of, 30°00′S, 151°40′E, on *Acacia* sp., 1980, *GNS* (BRIU3232NS); Clouds Ck, 30°10′S, 152°35′E, on small tree, 1978, *HS* (CBG7905564); Wollomombi Falls, 30°32′S, 152°03′E, on *Acacia* sp., 1982, *GNS* (BRIU3776NS); Port Macquarie, 31°26′S, 152°54′E, on *Avicennia marina*, 1977, *GNS* (BRIU2124NS); Walcha Road, 31°25′S, 151°30′E, on *Acacia* sp., 1982, *GNS* (BRIU3764NS); Cobak R. 31°57′S, 151°48′E, on *Casuarina* sp., 1982, *GNS* (BRIU3770NS); Gosford, Erina Ck, 33°25′S, 151°20′E, on *Casuarina glauca*, 1978, *JAE* (JAE 4722); Jenolan Caves, 33°48′S, 150°01′E, on *Acacia* sp., 1977, *JAE* (JAE 3180); Wombeyan Caves, 34°19′S, 149°58′E, on dead shrub, 1979, *HS* (CBG7907795); Nowra, 14 km N of, 34°48′S, 150°40′E, on tree, 1976, *HS* (3456); Bundanoon, 34°39′S, 150°18′E, on tree, 1954, *M. Tindale* (MEL9457); Bungendore, 12 km E of, 35°20′S, 149°28′E, on old bones, 1978, *JAE* (JAE 5465); Batemans Bay, 35°45′S, 150°10′E, on *Avicennia marina*, 1978, *GNS* (BRIU2170NS); Murunna Pt, 36°24′S, 150°05′E, on dead coastal shrub, 1978, *JAE* (JAE 4591); Twofold Bay, 37°05′S, 149°54′E, *White* (MEL 9456). **Victoria**: Lakes Entrance, 37°53′S, 148°00′E, 1901 (MEL 9465); Frankston, 38°11′S, 145°03′E, 1900 (MEL 9462); Traralgon, 8 km E of, 38°12′S, 146°32′E, on *Melaleuca* sp., 1975 *RF* (MEL1013204); Yarragon, Strzelecki Ra. 38°12′S, 146°04′E, on trees, 1973, *GB & R. C. Weeks* (H032292); Trida, Grand Ridge Rd, 38°19′S, 145°58′E, on trees, 1971, *GB & R. C. Weeks* (H032290); Gippsland, Foster 6·4 km NW of, 38°40′S, 146°13′E, on dead wood, 1968, *GB* (H032297). **Tasmania**: Trowutta, 41°02′S, 145°05′E, on *Pyrrhus* sp., 1981, *GK* 386/81.

subsp. ***ovalis*** (J. D. Hook. & Taylor) N. Stevens, **comb. nov.** Plate 10, fig. 2; Plate 15, fig. 5.

Ramalina ovalis J. D. Hook. & Taylor in *Lond. J. Bot.* **3**: 655 (1844). Type: Van Dieman's Land, *Gunn* s.n. (BM! – holotype; usnic acid). – *Ramalina calicaris* var. *ovalis* (J. D. Hook. & Taylor) Church. Bab. in J. D. Hook., *Flora Tasmaniae* **3**: 344 (1860). – *Ramalina ecklonii* var. *ovalis* (J. D. Hook. & Taylor) F. Wilson in *Pap. Proc. R. Soc. Tasm.* **1892**: 159 (1893). – *Ramalina yemensis* var. *ovalis* (J. D. Hook. & Taylor) Zahlbr., *Cat. Lich. Univ.* **6**: 529 (1930).

Thallus corticolous, green-grey, erect to subpendulous, 2–4(–5) cm long, exceptionally to 8 cm; branching sparse with one or two branches often constituting the whole thallus; branch width 8–20 mm, compressed, flat, apices blunt or rounded, small branchlets may occur at the apices; surface matt, membraneous and thin, wrinkled, or thick and ribbed with chondroid strands; pseudocyphellae sometimes present; holdfast delimited; soralia absent.

Apothecia laminal only, numerous, disc to 2·0 mm diam., plane to convex; margin entire, thin; spores ellipsoid or slightly fusiform, mostly curved, (10–)12–16 × 4–4·5 μm.

Chemistry. Usnic acid only.

Remarks. There is no record of the exact location of the collection of the type material of *R. ovalis* apart from Van Diemans Land. The obovate form of the branches was commented on by Hooker & Taylor (1844) in the type description – 'has the outline of *Fucus ovalis*' – and this morphology is common in Tasmanian material, but mainland specimens are more variable.

From the taxonomic nomenclature applied to this taxon in the past it appears most authors appreciated its affinity to the species *R. celastri* (= *R. yemensis*, = *R. ecklonii*).

Distribution and habitat. This temperate taxon occupies a broad band across Victoria, South Australia, and Western Australia in the latitudes 33°S to 38°S, and is found on the Bass Strait islands and in Tasmania along the north and eastern coast, latitudes 40°S–43°S (Fig. 20). It virtually replaces *R. celastri* subsp. *celastri* in these latitudes and is confined to areas of winter rainfall. It grows mainly in open-forest and tall shrubland communities.

Krog (in litt.) detected the occurrence of this broad taxon in collections of *R. celastri* from East Africa. Examination of the BM material from Tanzania, Moshi district (1440 m alt.) and Uganda (1950–2100 m alt.) showed that thalli with the same morphology as *R. celastri* subsp. *ovalis* grow in these open-forest areas. This taxon also occurs in New Zealand at comparable latitudes to those where it is found in Australia.

The main phorophytes of *R. celastri* subsp. *ovalis* are *Acacia pycnantha, A. melanoxylon, A. acuminata, A. longifolia, A. dealbata,* and *Lycium ferocissimum, Bursaria spinosa, Banksia marginata, Casuarina stricta, Callitris* sp., and *Pyrrhus, Populus, Malus*, and *Prunus* spp.

World distribution. Africa and Australia.

New South Wales: Neville, 33°43′S, 149°13′E, on *Acacia* sp., 1980, *GNS* (BRIU3302NS); Crookwell, 34°28′S, 149°29′E, on *Acacia* sp., 1980, *GNS* (BRIU3233NS). **Victoria**: Marlo, 37°48′S, 148°32′E, on *Leucopogon* sp., 1980, *GNS* (BRIU3221NS); Korumburra, Coal Ck, 38°25′S, 145°48′S, on *Acacia* sp., 1980, *GNS* (BRIU3248NS); Wilsons Prom, N of, 38°45′S, 146°08′E, on *Acacia* sp., 1980, *GNS* (BRIU3219NS); Crib Pt, Westernport Bay, 38°22′S, 145°10′E, on *Avicennia marina*, 1978, *GNS* (BRIU2346NS); Gunnamatta Beach, 38°23′S, 144°45′E, on dune shrub, 1976, *RF* (MEL1025871); Ballarat, 20 km WNW of, 37°30′S, 143°44′E, on *Pinus* sp., 1975, *E. M. Canning* (CBG8100893); Portland, 38°21′S, 141°36′E, 1947, *A. C. Beauglehole* (MEL1020517). **South Australia**: Oodlawirra, 5 km W of, 32°53′S, 139°03′E, on *Muellenbeckia* sp., 1969, *RWR* (BRIU1632RR); Eyre Peninsula, W of Lake Newland, 33°22′S, 134°53′E, 1967, *N. N. Donner* (AD97539274); Yorke Peninsula, Cape Elizabeth, 34°08′S, 137°27′E, 1969, *B. Copley* (AD97414422); Port Rickaby, S. of, 34°41′S, 137°29′E, 1974, *J. Z. Weber* (AD97648159); Springton, 14 km SE of, 34°39′S, 139°06′E, on *Callitris* sp., 1974, *JAE* (JAE 481); Mt Lofty Ra., Clarendon, 35°07′S, 138°38′E, 1968, *V. Cruickshank* (AD97418421); Trent Hill, 35°36′S, 138°12′E, on *Casuarina* sp., 1968, *RWR* (BRIU1458RR); Naracoorte, 36°58′S, 140°45′E, *D. Hunt* (CBG067824); Kangaroo I, W of Kingscote airport, 35°39′S, 137°38′E, on *Eucalyptus* sp., *R. D. Seppelt* (MEL1024502). **Western Australia**: Boyup Brook, 33°50′S, 116°22′E, on *Malus* sp., 1974, *K. M. Allan*; Lake King, 33°05′S, 119°40′E, on twigs, 1980, *D. Richardson* (PER000996); Northcliffe, Beedalup Falls Rd, 34°38′S, 116°07′E, on dead tree, 1973, *B. Muir* (N. Sammy Herb); Recherche Archipelago, Peak I, 34°00′S, 122°50′E, on *Acacia acuminata*, 1950, *J. H. Willis* (MEL 10025); Long I, 34°03′S, 121°58′E, on *Melaleuca* sp., 1950, *J. H. Willis* (MEL 10020). **Bass Strait**: Curtis I, 39°29′S, 146°39′E, 1971, McCoy Expedition, (MEL40274); Furneaux Group: Forsyth I, 40°38′S, 148°25′E, on *Acacia* sp., 1976, *JW* (MEL1516801). **Tasmania**: Stanley, The Nut, 40°45′S, 145°15′E, on *Bursaria spinosa*, 1965, *J. H. Willis* (MEL 7588); Devonport airport, 41°10′S, 145°20′E, on *Poplar* sp., 1980, *GNS* (BRIU3236); Avoca, 41°48′S, 147°40′E, on *Prunus* sp., 1978, *GK* 2/78; Sorrell-Nugent Rd, 42°46′S, 147°39′E, on briars, 1964, *GB & JC* (H032314).

15. ***Ramalina inflata*** (J. D. Hook. & Taylor) J. D. Hook. & Taylor

in J. D. Hook., *Flora Antarctica* **1**: 194 (1845).

Cetraria inflata J. D. Hook. & Taylor in *Lond. J. Bot.* **3**: 646 (1844). Type: Lord Auckland Islands, *Hooker* s.n. (FH! – holotype; BM! – isotype; divaricatic acid and usnic acid). – *Fistulariella inflata* (J. D. Hook. & Taylor) Bowler & Rundel in *Mycotaxon* **6**: 195 (1977).

subsp. ***inflata*** Plate 10, figs 5–6; Plate 14, fig. 5.

Ramalina tasmanica Nyl. in *Bull. Soc. Linn. Normandie* II, **4**: 162 (1870) type: Australia, Tasmania, *J. D. Hooker* s.n. (H! – holotype [H-NYL 36849 ex hb. Churchill Babington]; divaricatic acid and usnic acid). Plate 14, fig. 6.

Ramalina knightiana Zahlbr., *Cat. Lich. Univ.* **6**: 494 (1930); *Ramalina subgeniculata* Knight in *Trans. Linn. Soc. Lond.* (Bot.) **2**: 50 (1882), non Nyl. (1870) (Art 64.1). Type: Australia, New South Wales, near Sydney, *Knight* s.n. (WELT! – holotype; divaricatic acid, sekikaic acid, and usnic acid).

Thallus corticolous, green to pale green, caespitose, erect 1–2(–3) cm high; branching subdichotomous or irregular; branch width 1–3 mm, branches hollow, terete, inflated and perforate; perforations round to elongate, medullary hyphae continuous, loosely woven across central cavity or compressed against the inner cortex wall either loosely or densely; surface matt to shiny, smooth, rarely pseudocyphellate; holdfast delimited; soralia absent.

Apothecia common, terminal on main branches and on short subapical lateral branches, often spurred; disc 2–5 mm diam., always concave initially, innate at branch apices, becoming plane at maturity; margin entire, thin often indistinct; spores broadly ellipsoid, straight or curved, 12–16 × 4–5(–6) μm.

Chemistry. Divaricatic acid, ± nordivaricatic acid, ± sekikaic acid, and usnic acid.

Remarks. Sterile specimens of this taxon are usually larger than fertile thalli, occurring either as greatly inflated, pulvinate, thalli or having elongate branches with perforations evenly distributed along the lower surface and extending to the attenuate apices.

A small morphotype of *R. inflata* subsp. *inflata* found in Tasmania was named *R. tasmanica* Nyl.; the type material contains divaricatic acid. Subsequent collections from Tasmania bearing this name have been found to contain salazinic acid and belong to *R. fissa*. The type material of *R. knightiana* Zahlbr. is a very finely branched specimen of *R. inflata* subsp. *inflata* collected in the neighbourhood of Sydney; its morphology closely resembles the New Zealand species *R. geniculata* and was originally named *R. subgeniculata* by Knight.

The synonomy of *R. inflata* and *R. geniculata* has been the subject of debate by several lichenologists (Howe, 1913–14; Landrón, 1972; Bowler & Rundel, 1977). An examination of the types of both of these species during the present study has shown them to contain the same acid (divaricatic) but to differ morphologically. More material from New Zealand (from which country the type of *R. geniculata* was collected) would need to be examined to evaluate the amount of phenotypic plasticity displayed by this taxon and to compare the morphotypes with *R. inflata* ecophenotypes, in order to establish if both taxa intergrade with one another.

In many respects the morphology and habitat requirements of the East African taxon *R. calcarata* Krog & Swinscow come close to the Australian specimens of *R. inflata* subsp. *inflata*, but the presence of salazinic acid in the hymenium of the former taxon distinguishes the two. A tan coloration on the lower surface of some specimens of *R. calcarata* was mentioned by Krog & Swinscow (1974) and this colour occasionally occurs on the Australian material of *R. inflata* subsp. *inflata*. However discoloration of the thallus is not common and is not regarded as of any taxonomic significance. The original protologue of *R. inflata* contains the comment: 'sometimes stained with dark blood red', but this colour is rarely evident on specimens. However black patches on the thallus of *R. pusilla* Le Prev. ex Duby., have been commented upon by Krog & Østhagen (1980).

Distribution and habitat. The distribution of *R. inflata* subsp. *inflata* (Figs 21, 22) extends along the warm to cool temperate section of the eastern and south-eastern Australian coastal belt and into the cool/cold temperate region of Tasmania. The most northern occurrence of this taxon is

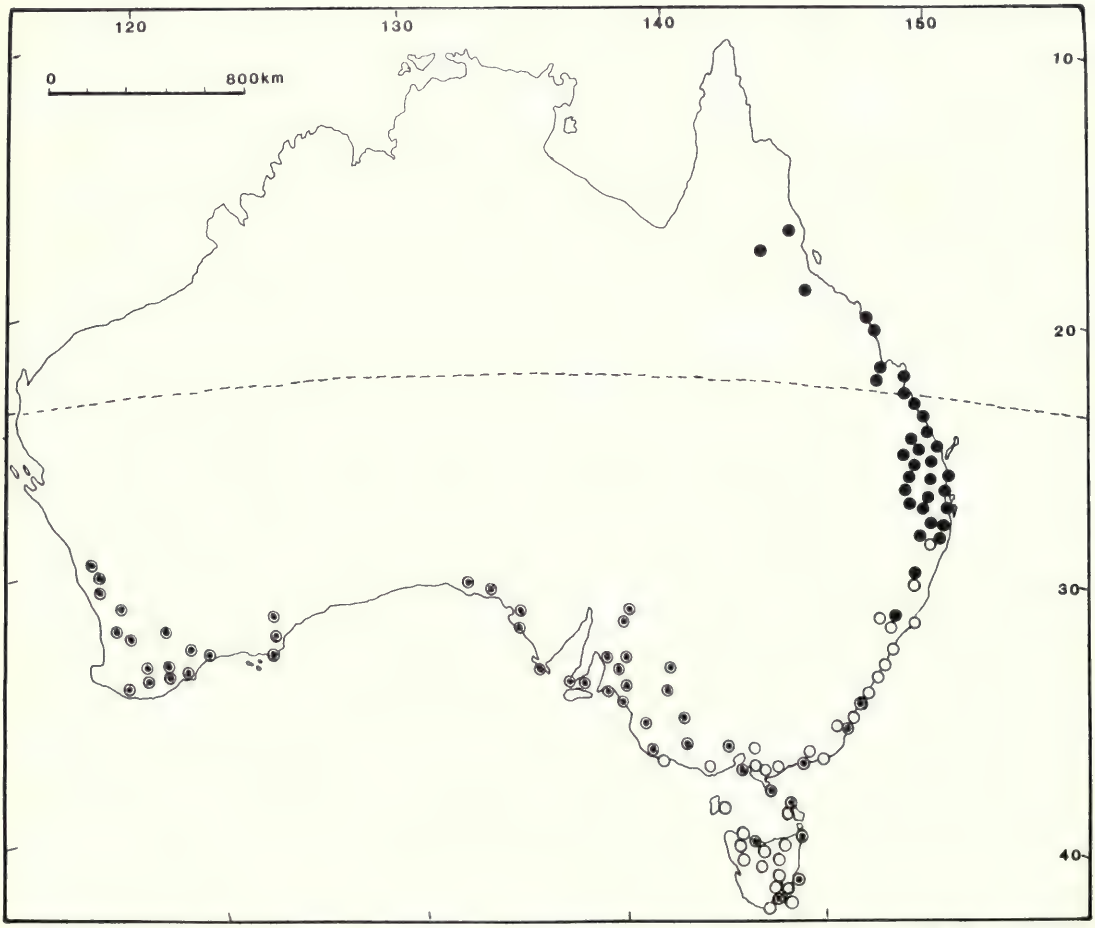


Fig. 21 Distribution of *R. inflata* subsp. *inflata* ○, subsp. *perpusilla* ●, and subsp. *australis* ◉.

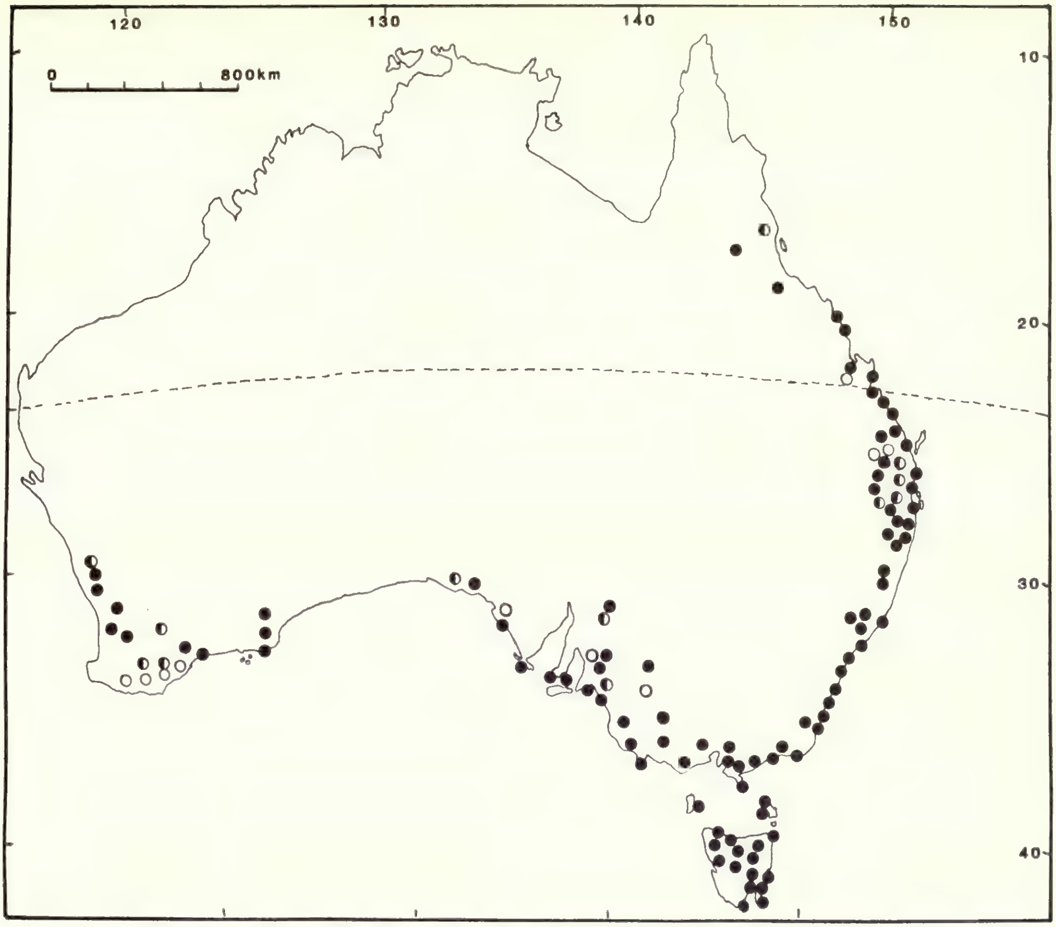


Fig. 22 Distribution of *R. inflata* complex: ● divaricatic acid race; ○ sekikaic acid race.

in the mountains at elevations of 1000 m in the area 28°–30°S latitude. This is an area where intermediates between the morphology of the rain-forest ecotype of *R. inflata* subsp. *perpusilla* and the morphology of *R. inflata* subsp. *inflata* occur. At 30°S latitude (Wollomombi Falls, elevation 1000 m) *R. inflata* subsp. *inflata* grows on *Acacia* in open forest communities growing on metamorphic rock, and the thalli are typical; at 32°S latitude (Barrington Tops, a basalt range) thalli collected from rain-forest areas were difficult to place in either taxon, indicating that the microhabitat as well as climatic conditions may be influencing these two subspecies.

The most common phorophytes for *R. inflata* subsp. *inflata* are *Acacia* and *Casuarina* spp.

World distribution. South Africa, Australia, Auckland Island, Brazil, and Venezuela. [Unconfirmed reports are from China (Zahlbruckner, 1930), North America (Howe, 1914), West Indies (Landrón, 1972), and Hawaii (Magnusson, 1955)].

New South Wales: Undercliff Falls, 28°38′S, 152°10′E, on *Acacia* sp., 1980, *GNS* (BRIU3028A.NS); Wollomombi Falls, 30°30′S, 152°03′E, on *Acacia* sp., 1982, *GNS* (BRIU3639NS); Barrington Tops, 32°00′S, 151°30′E, on rain-forest tree, 1982, *GNS* (BRIU3636NS); Scone, 12 km W of, 32°05′S, 150°55′E, on bush, 1982, *GNS* (BRIU3635NS); Tuncurry, 32°10′S, 152°27′E, on *Casuarina* sp., 1982, *GNS* (BRIU3648NS); Erina Ck, 33°25′S, 151°21′E, on *Casuarina glauca*, 1978, *JAE* (JAE4705); Towra Pt, 34°02′S, 151°13′E, on *Casuarina* sp., 1977, *CS* (BRIU63CS); Barrengarry Mt, 34°41′S, 150°34′E, on tree, 1976, *JAE* (JAE2714); Currowan State Forest, 35°39′S, 150°08′E, on *Acacia* sp., 1977, *JAE* (JAE3576); Batemans Bay, 35°42′S, 150°10′E, 1970, *ED* (0); Batemans Bay, on *Avicennia marina*, 1978, *GNS* (BRIU2172NS); Wallaga Lake, 36°23′S, 150°03′E, on *Casuarina* sp. n., 1978, *JAE* (JAE 4543); Spring Ck

Gap, 37°30′S, 148°20′E, on *Acacia* sp., 1978, *JAE* (JAE5156); Marlo, 37°48′S, 148°32′E, on *Acacia* sp., 1978, *GNS* (BRIU3282NS); Cape Conran, 37°49′S, 148°45′E, on *Leptospermum* sp., 1983, *GNS* (BRIU3676NS); Rodondo I, 39°15′S, 146°23′E, 1970, *J. Kirkpatrick* (MEL39969); Cape Patterson, 38°40′S, 145°35′E, on *Acacia pycnantha*, 1963, *RF & Smith* 3413; French I, Tankerton Rd, 38°20′S, 145°20′E, *S. Filson* (MEL1026170); Healesville, 37°39′S, 145°32′E, on twigs, 1974, *RB* (MEL1013089); Mt Richmond Nat. Park, 38°18′S, 141°30′E, 1978, *AA* (BRIU4312NS). **Bass Strait**: Kents Group: Erith I, 39°28′S, 147°13′E, on *Beyeria leschenaultia*, 1970, *JW* (MEL1012899). **Tasmania**: Rocky Cape, 40°51′S, 145°31′E, 1975, *D & M. Cook* (H032566); Yolla, 41°09′S, 145°40′E, on *Malus* sp., 1980, *GNS* (BRIU3239NS); Mt Barrow, 41°23′S, 147°25′E, on *Acacia* sp., 1966, *GB* (H032678); Liffey Falls, 41°41′S, 146°47′E, on *Acacia* sp., 1969, *GB & JC* (H032752); Tarraleah, 42°15′S, 146°26′E, on *Acacia dealbata*, 1980, *GK* 347/80; Mt Faulkner, 42°48′S, 147°12′E, on *Acacia* sp., 1965, *GB & JC* (H032762).

subsp. ***perpusilla*** (Stirton) N. Stevens, **comb. nov.** Plate 10, figs 3–4; Plate 14, fig. 3.

Ramalina perpusilla Stirton in *Proc. R. Soc. Vict.* **17**: 68 (1881). Type: Australia, Queensland, Brisbane, *Bailey* 113 (BRI! – lectotype; herein designated, left hand specimen; divaricatic acid and usnic acid).

Ramalina minuscula var. *alba* C. Knight ex Shirley in *Proc. R. Soc. Qd* **5**: 103 (1888). Type: Australia, Queensland, Mt Perry, *Keys* 91 (WELT! – lectotype; sekikaic acid and usnic acid). Plate 15, fig. 7.

Ramalina geniculata var. *compacta* Müll. Arg. in *Bull. Herb. Boissier* **4**: 88 (1896). Type: Australia, Queensland, Toowoomba, *Hartmann* s.n. (G! – lectotype designated here; divaricatic acid and usnic acid).

Thallus corticolous, green to pale green, often with white lower surface, caespitose, erect, 1–2(–3) cm high; branching subdichotomous, branch width 0·5–2·0 mm, varying in the amount of inflation, terete to almost flat, sparingly to moderately perforate, the perforations on the lower surface only, small and round, extending to the apices on sterile branches; medullary hyphae sparse and adhering to the inner cortex wall either loosely or densely compacted in totally inflated specimens or thick and felty in compressed thalli; surface matt or shiny, smooth to rugose; very rarely pseudocyphellate; holdfast delimited or diffuse; soralia absent.

Apothecia sparse to numerous, subterminal on geniculate branches or terminal on main and short lateral branches, spurred, or in the axils of bifurcating branches, disc usually less than 2·0 mm diam., plane to convex; margin entire, well defined, rarely indistinct; spores ellipsoid, straight, rarely curved, (8–)10–14(–16) × 4–5 μm.

Chemistry. Divaricatic acid ± trace sekikaic acid, ± nordivaricatic acid or sekikaic acid only, or rarely sekikaic acid, 4'-0-demethylsekikaic acid, an unknown and usnic acid.

Remarks. The type material of *R. inflata* subsp. *perpusilla* comprises four specimens with the number 113 apparently covering three of the specimens and the number 259 covering the fourth specimen. The left hand specimen contains divaricatic acid and is the most likely single specimen that number 113 could refer to (Plate 14, fig. 3). The middle and right hand top specimens contain sekikaic acid as does specimen 259. The left-hand specimen has been selected as lectotype for this taxon because it appears to conform best with the original protologue. As the majority of specimens collected during this study contain divaricatic acid as the major acid, the choice of a lectotype which contained divaricatic acid seemed appropriate.

The only locality given for the type collection is Brisbane River. In describing this species later, Shirley (1888) gave the information ‘Hocking's Nursery, Brisbane River’. It is not clear however, whether the specimens were growing on native trees in the area, or on the mangroves, or were found on one of the nursery trees, which could have come from elsewhere. Specimens which produce sekikaic acid only have not been found on mangroves; they are usually found in dry inland situations, which would indicate that the type material possibly grew on a plant which had come from another location. This problem remains unsolved and the true type locality is not known.

Ramalina minuscula var. *alba* was collected at Mt Perry, a dry open-forest area in southern Queensland. The type material consists of 11 carded specimens all of which contain sekikaic acid.

Ramalina geniculata var. *compacta* was collected in the Toowoomba area. The material comprises six specimens on a card (a, b, c, d, e, f); b and d contain divaricatic acid whereas a, c, e and f contain sekikaic acid. Specimen b is designated lectotype as it conforms best with the original protologue and contains divaricatic acid, consistent with the type of *R. inflata* subsp. *perpusilla* with which it is synonymous. As Toowoomba is an inland region about 130 km from the coast, the presence of sekikaic acid specimens as well as divaricatic acid specimens is not unusual because fresh collections made during the present study from inland areas always contained sekikaic acid thalli as well as divaricatic acid thalli. The sekikaic acid race has not been given any taxonomic rank because of the co-existence of both divaricatic and sekikaic acids in many of the thalli.

The morphology of the East African taxon *R. consanguinea* Müll Arg. from the mangroves resembles *R. inflata* subsp. *perpusilla* specimens from the mangrove communities. Both produce apothecia which are plane to convex but never concave, and the former taxon has short slender side branches and spinules on the main branches, a feature sometimes present on Australian specimens. *Ramalina consanguinea*, however, contains both divaricatic acid and norstictic acid and produces large spores 20–25(–28) × 4–5(–6) μm, which sets it apart from *R. inflata* subsp. *perpusilla*.

Ramalina pumila Mont., an Asian taxon, appears to be close to the Australian taxon morphologically, but its chemistry (evernic acid with trace amounts of sekikaic acid) sets the two taxa apart.

Distribution and habitat. Ramalina inflata subsp. *perpusilla* has a distribution range from the tropics to the subtropics (Figs 21, 22). The highly variable morphology found in this taxon over this range is ecophenotypic. Three distinct habitats are considered to explain the ecotypes that occur, e.g. (1) the mangrove habitat, (2) the open-forest habitat, and (3) the rain-forest (closed-forest) habitat.

(1) The mangrove habitat: Specimens of *R. inflata* subsp. *perpusilla* collected from mangrove communities along the Queensland coastline from Hallidays Bay (latitude 20°56′S) to Moreton Bay (latitude 28°S) are usually small and caespitose with elongate perforations spread irregularly along the lower surface; short spinules are sometimes present on the main branches and the margins of the apothecia are very distinct. North of latitude 23°50′S (Gladstone), 80% of the specimens were found to contain only divaricatic acid whereas 45% of specimens south of Gladstone contained divaricatic acid and trace amounts of either sekikaic acid or nordivaricatic acid.

The main mangroves which act as phorophytes for this taxon are *Ceriops tagal* and *Rhizophora stylosa*, and when these mangroves reach their southern distribution limit at latitude 28°S, *R. inflata* subsp. *perpusilla* ceases to occur along the coastline.

(2) The open-forest habitat (including disturbed habitats): These dry inland areas lie between the maritime and the montane-rain-forest environments and collections of *R. inflata* subsp. *perpusilla* from such habitats are scattered from latitudes 18°S–27°S. The thalli are very small with a maximum size of less than 1·0 cm high; they are usually green or pale green with a smooth, shiny surface, wholly inflated; perforations are round and evenly distributed on the lower surface of the thallus; the branches are either tightly packed together with numerous terminal apothecia covering the thallus (Plate 10, fig. 3) or are palmate at the base, dividing into several branches which bear subterminal apothecia or apothecia situated in the axils of bifurcating branches.

In this open-forest habitat more than 50% of the population contains sekikaic acid only with the remainder containing divaricatic acid ± trace amounts of sekikaic acid. The most common phorophytes in such habitats are the small thorny shrubs *Citriobatus pauciflora* and *Acalypha capillipes*. They grow on basaltic soils in open areas experiencing full sunlight and varying humidity; areas which in some respects resemble the open mangrove community where *Ceriops tagal* grows.

(3) The rain-forest habitat: Pockets of rain-forest where this particular ecotype occurs extend from the tropics to the subtropics along the Eastern Highlands (viz. Atherton Tableland (17°S), Mt Surprise (19°S), Bunya Mts (27°S), McPherson Ra. (28°S), and Dorrigo Plateau (30°S). Specimens of *R. inflata* subsp. *perpusilla* from this habitat tend to be loosely branched, 2–3 cm

long, with a pale lower surface; branching is subdichotomous with the branches less inflated, even partially compressed, and more rugose than those of the taxa from more exposed habitats; the perforations are small, slightly elongate and sparse; the apothecia are usually terminal and subterminal, with some tendency to be innate when immature but becoming plane at maturity.

The majority of the rain-forest specimens contain only divaricatic acid, with a small proportion producing trace amounts of either sekikaic acid or nordivaricatic acid in addition to divaricatic acid. The main phorophytes are various species of rain-forest tree, including *Araucaria cunninghamii* and *Eugenia* sp., and also *Acacia melanoxylon* and *A. orrites* which fringe the rain-forest borders.

Although this taxon occupies three distinct habitats, there is total intergradation of morphotypes from one environment to another which prevented any division of the group being made based on microhabitat morphology. Chemistry was not able to be used taxonomically, as variation from divaricatic acid only in the thallus to divaricatic acid + trace sekikaic acid to sekikaic acid only was found to occur.

One inflated specimen collected from Lake Eacham, Atherton Tableland (JAE 2427), has not been included in this taxon; it is a large specimen (4 cm long), partially inflated, partially compressed (which is normal for the rain-forest habitat in which it grew) with white punctiform pseudocyphellae along the branches. The acids present are sekikaic, homosekikaic, 4'-0-demethylsekikaic, and an unknown. This chemistry differs from that produced by the majority of the taxa in this group but it is similar to the acids found in a few inland specimens of *R. inflata* subsp. *perpusilla*. The presence of white pseudocyphellae, however, is quite distinct. As no other specimens have been collected from Atherton Tableland, or elsewhere, the specimen remains unnamed at present.

World distribution. Australia.

Queensland: Tinaroo Dam, 17°16′S, 145°34′E, on *Araucaria cunninghamii*, 1983, *GNS* (BRIU4167NS); Forty Mile Scrub, 18°03′S, 144°53′E, on thorny shrub, 1983, *GNS* (BRIU4114NS); Burdekin R, Big Bend, 19°15′S, 146°12′E, on thorny bush, 1983, *GNS* (BRIU4154NS); Hallidays Bay, 20°56′S, 149°01′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4118); Eimeo Beach, 21°05′S, 149°13′E, on *Ceriops tagal*, 1976, *GNS* (BRIU2221NS); St Lawrence, 22°20′S, 149°32′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4105NS); Marlborough, 22°50′S, 149°51′E, on thorny bush, 1983, *M. Olsen* (BRIU4157NS); Port Alma, 23°35′S, 150°42′E, on *Rhizophora stylosa*, 1975, *RWR* (BRIU696RR); Gladstone, 23°50′S, 151°16′E, on *Ceriops tagal*, 1980, *GNS* (BRIU3653NS); Cania Gorge, 24°38′S, 150°56′E, on *Casuarina* sp., 1984, *NCS* (BRIU4343NS); Bundaberg, The Hummock, 24°51′S, 152°26′E, rainforest tree, 1977, *I. R. Telford* (CBG7702460); Goodnight Scrub, 25°15′S, 151°50′E, on thorny bush, 1981, *P. Forster* (BRIU3640NS); Toogoom, 25°15′S, 152°40′E, on *Callitris* sp., 1983, *GNS* (BRIU4150NS); Coalston Lakes, 25°35′S, 151°55′E, on thorny bush, 1980, *RWR* (BRIU3586RR); Narayan, 25°48′S, 151°10′E, on shrub, 1980, *RWR* (BRIU2197RR); Barambah Ck, 25°40′S, 151°45′E, on shrub, 1982, *NCS* (BRIU3606NS); Mt Blandy, 25°40′S, 151°38′E, on thorny bush, 1980, *P. Forster* (BRIU3641NS); Lake Cootharaba, 26°18′S, 152°58′E, on *Bruguiera* sp., 1978, *GNS* (BRIU3620NS); Maleny, 26°46′S, 152°51′E, on *Acacia* sp., 1982, *GNS* (BRIU3568NS); Bunya Mts, 26°50′S, 151°40′E, on rainforest shrub, 1979, *GNS* (BRIU3009NS); Mt Mee, 27°06′S, 152°42′E, on *Citriobatus pauciflora*, 1979, *GNS* (BRIU3654NS); Stradbroke I, 27°25′S, 153°27′E, on *Lumnitzera racemosa*, 1977, *GNS* (BRIU2118NS); Lake Broadwater Park, 27°21′S, 151°05′E, 1983, *B. Ballingall* 981; Worlds End Pocket, 27°37′S, 152°55′E, on *Acalypha capillipes*, 1983, *P. Forster* (BRIU3709NS); Toowoomba, Cooby Ck Rd, 27°23′S, 151°38′E, on *Citriobatus pauciflora*, 1983, *GNS* (BRIU3685NS); Pittsworth, 27°45′S, 151°38′E, on *Carissa ovata*, 1983, *M. Olsen* (BRIU3762NS); Coochiemudlo I, 27°35′S, 153°20′E, on *Rhizophora stylosa*, 1981, *GNS* (BRIU3623NS); Coomera I, 27°55′S, 153°25′E, on *Rhizophora stylosa*, 1979, *GNS* (BRIU3649NS); Tamborine Mt, 27°55′S, 153°12′E, on rain-forest tree, 1979, *GNS* (BRIU3010NS); Mt Cordeaux, 28°03′S, 152°23′E, on rain-forest tree, 1979, *GNS* (BRIU3029NS); Springbrook, 28°15′S, 153°16′E, on rain-forest tree, 1982, *RWR* (BRIU2567RR); O'Reillys, 28°15′S, 153°08′E, on rain-forest tree, 1983, *GNS* (BRIU3718NS); The Head, 28°18′S, 152°27′E, on rain-forest tree, 1980, *GNS* (BRIU3621NS); Kelvin Falls, 28°23′S, 152°06′E, on *Casuarina* sp., 1980, *NCS* (BRIU3286A.NS). **New South Wales**: Wiangaree, 28°25′S, 153°08′E, on rainforest tree, 1978, *GNS* (BRIU3028NS); Undercliff Falls, 28°38′S, 152°10′E, on *Acacia* sp., 1980, *GNS* (BRIU3651NS); Cherry Tree State Forest, 28°54′S, 153°01′E, on vine, 1983, *B. Ballingall* (BRIU3646NS); Clouds Ck, State Forest, 30°10′S, 152°35′E, on shrub, 1978, *HS* (CBG9705565); Mt Dorrigo, 30°20′S, 152°40′E, on rain-forest tree, *JAE* (JAE 3447).

subsp. ***australis*** N. Stevens, **subsp. nov.** Plate 10, fig. 7.

Thallus corticolus et saxicolus, virido-griseus parvus caespitosus rigidus erectus, usque ad 1·0 cm altus, ramificatione nulla vel sparsa, ramis e basi exorientibus; rami lati usque ad 10 mm, valde cavi; superficies impolita, laevigata et tenui vel rugosa et crassi; soralia nulla. Apothecia numerosa, terminalia, non calcarata, primum immersa, demum plana; discus usque ad 10 mm in diametro; sporae late ellipsoideae, curvatae aut rectae, (10–)13–14 × 4–5(–6) μm. Acidum divaricaticum ± sekikaicum aut sekikaicum et usnicum continens.

Holotype: Australia, Western Australia, Moora-Perth Road on *Acacia* sp. 6 August 1984, *G. N. Stevens* 4315 (MEL 1048089!).

Thallus corticolous and saxicolous, greenish-grey, small caespitose, rigid, erect, usually to 1·0 cm high, branching sparse, at the base only; branches broad, up to 10 mm wide, highly inflated, perforations large, round to elongate and often splitting apart revealing a sparse medulla and internal chondroid strands forming a reticulate fibrose surface on the inner cortex wall; surface matt, smooth and thin to rugose and extremely coarse, rarely pseudocyphellate; holdfast delimited; soralia absent, although some rock specimens with eroded apices appeared pseudosorediate.

Apothecia numerous, terminal, not spurred, sometimes laminal; disc up to 5·0 mm, exceptionally to 10 mm diam., concave initially, remaining so or becoming plane; margin entire, inrolled; spores broadly ellipsoid, mainly curved, some straight, (10–)12–14 × 4–5(–6) μm.

Chemistry. Divaricatic acid ± sekikaic acid or sekikaic acid only and usnic acid.

Remarks. Two acid races occur in *R. inflata* subsp. *australis*, (1) a divaricatic acid race and (2) a sekikaic acid race. The only name which has been applied to this taxon in the past is *R. pusilla*, a northern hemisphere *Ramalina* which contains sekikaic acid with salazinic acid in small amounts (Krog & Swinscow, 1974).

Krog & Østhagen (1980) reported that one specimen of *R. pusilla* from Hierro, Canary Islands, contained salazinic acid only, which indicates that some relationship could exist between the taxa which produce sekikaic acid and *R. fissa*, which produces salazinic acid only. Partly because of this, *R. fissa* is placed in the *R. inflata* complex. Morphologically the sekikaic acid thalli of *R. inflata* subsp. *australis* seem closer to the salazinic acid *R. fissa* thalli than to the divaricatic acid thalli. However, the presence of divaricatic acid and sekikaic acid in the same thallus shows the close connection between the two depside races, thus preventing the sekikaic acid race being separated into a separate taxon from the divaricatic acid race.

See Table 11 for a comparison of the three subspecies.

Distribution and habitat. Ramalina inflata subsp. *australis* occurs in the temperate region of mainland Australia and in the drier north and east coastal areas of cool-temperate Tasmania (Figs 21, 22). The two chemical races which occur in this taxon are sympatric over most of their range, although only the divaricatic acid race occurs coastally. No sekikaic acid thalli were found in Tasmania.

Within its range *R. inflata* subsp. *australis* exhibits a variety of ecophenotypes. In the drier inland regions of South Australia extremely small thalli are found bearing large terminal apothecia which obscure the branches (Plate 10, fig. 7). Both divaricatic acid and sekikaic acid races occur in such areas, with a predominance of the latter race. In some habitats this taxon produces a single inflated branch resembling a small round balloon.

The divaricatic acid race also occurs on rock substrates, e.g. sandstone (Mt Arapiles and the Grampians) and on trachyte (Hanging Rock). Although the morphology of the saxicolous thalli differs from the corticolous thalli, the differences are regarded as the result of change in substrate rather than genotypic, e.g. the thalli are much reduced in size, occurring as small button-like growth forms in colonies; they produce prominent apothecia between sterile branches. This rock morphotype resembles the northern hemisphere saxicolous taxon *R. mediterranea* Magnusson, but the Mediterranean species contains evernic acid. It could be argued that this change in substrate and morphology warrants the erection of a new species for this rock morphotype. However, it is regarded as an ecophenotype of *R. inflata* subsp. *australis*.

Table 11 Comparison of morphological and chemical character and substrate preference of the three subspecies in the *Ramalina inflata* complex.

Character	subsp. *perpusilla*	subsp. *inflata*	subsp. *australis*
Usual size of thallus	1·5–2·0(–3·0) cm long	2·0–3·0(–4·0) cm long	1·0 cm long
Degree of inflation	almost compressed to fully inflated	fully inflated	extreme inflation
Perforations	small, round, or slit-like	large, round, elongate	large, oval, usually split open
Medullary hyphae	dense and continuous to loosely woven and patchy	rarely dense, loosely woven and patchy	sparse, adhering to wall of chondroid cylinder
Position of apothecia	mainly subterminal, terminal	mainly terminal	terminal and laminal
Size of apothecia	up to 2·0 mm diam.	between 2–5 mm diam.	5·0(–10) mm diam.
Shape of apothecia	plane, rarely convex	concave to plane	concave rarely plane
Spurred or not	spurred	sometimes spurred	not spurred
Form of margin	well defined	indistinct to well defined	well defined and inrolled
Spore shape	straight, rarely curved	straight or curved	straight to strongly curved
Spore size	(8–)10–14(–16) × 4–5 μm	12–16 × 4–5(–6) μm	(10–)12–16 × 4–5(–6) μm
Chemistry	divaricatic acid ± either nordivaricatic or sekikaic acids or sekikaic acid only	divaricatic acid ± nordivaricatic acid or ± sekikaic acid	divaricatic acid ± sekikaic acid or sekikaic acid only
Substrate	bark	bark	bark or rock

Ramalina inflata subsp. *australis* is mainly corticolous and grows on various tree species. Exotic phorophytes are *Pinus, Populus,* and *Malus*; native phorophytes include *Acacia, Casuarina, Leucopogon,* and *Melaleuca* spp.

World distribution: Australia.

New South Wales: Batemans Bay, 35°42′S, 150°10′E, on *Avicennia marina*, 1978, *GNS* (BRIU2172NS); Murunna Pt, 36°23′S, 150°03′E, on coastal shrub, 1978, *JAE* (JAE 4592). **Victoria**: Marlo, 37°48′S, 148°32′E, on *Melaleuca* sp., 1978, *GNS* (BRIU3201NS); Wilsons Prom., N of, 38°45′S, 146°08′E, on *Acacia* sp., 1980, *GNS* (BRIU3218NS); Mt Macedon, Hanging Rock, 37°23′S, 144°36′E, on trachyte, 1976, *GNS* (BRIU3128NS); Spargo Ck, Korwerigaboora Springs, 37°30′S, 144°00′E, 1965, *M. Allender* (MEL1026135); Triodea Hill, 37°57′S, 141°19′E, on *Banksia* sp., 1965, *RF* (MEL1026193); Drik Drik, 38°00′S, 141°18′E, 1952, *A. C. Beauglehole* (MEL544971); Rocket Lake, 34°39′S, 141°48′E, 1970, *ED* (0); Big Desert, 35°22′S, 141°13′E, 1970, *ED* (0); The Grampians, 37°08′S, 142°26′E, on rock, *RF* (MEL1026047); Dimboola Nat. Park, 36°20′S, 142°01′E, 1949, *A. C. Beauglehole* (MEL1020493). **South Australia**: Oodlawirra, 5 km W of, 32°53′S, 139°04′E, on *Muellenbeckia* sp., 1969, *RWR* (AD97649267); Yunta, 40 km S of, 32°59′S, 138°50′E, 1971, *N. N. Donner* (AD97407411); Blanchetown, 13 km W of, 34°21′S, 139°29′E, 1973, *J. Z. Weber* (AD97647391); Naracoorte, 25 km SE of, 36°58′S, 140°45′E, 1969, *J. Z. Weber* (AD97417116); York Peninsula, Treasure Cove, 35°00′S, 137°25′E, on dead shrub, 1979, *JAE* (JAE 6367); Eyre Peninsula, Streaky Bay, 40 km SE of, 32°48′S, 134°13′E, 1967, *N. N. Donner* (AD97648422); Colona Homestead, 31°38′S, 132°04′E, 1947, *J. H. Willis* (MEL1026176); Yalata Road House, 5 km W of, 31°39′S, 129°03′E, on bushes, 1980, *AA* (BRIU4345NS). **Western Australia**: Three Springs, 5 km from, 29°32′S, 115°46′E, 1969, on edge of salt lake, *R. A. Saffrey* (PER000427); Winchester, 8 km W of, 29°46′S, 115°56′E, on tree, 1966, *P. G. Wilson* (PER000426); Toodyay-Bindoon Rd, 31°25′S, 116°15′E, on *Acacia* sp., 1984, *GNS* (BRIU4316NS); Pt Mt Henry, Perth, 32°02′S, 116°05′E, on *Dryanda sessilis*, 1970, *N. Sammy*; Beverley, 17 km S of, 32°10′S, 116°56′E, on *Acacia* sp., 1984, *GNS* (BRIU4319NS); Hyden, The Humps, 32°19′S, 118°57′E, on granite rock, 1972, *N. Sammy*; Kondinin Forestry Reserve, 32°30′S, 118°24′E, on bushes, 1967, *GB* 67/366; Cranbrook 17 km N of, 34°15′S, 117°37′E, on *Casuarina* sp., 1984, *GNS* (BRIU4314NS); Lake Muir, E side, 34°29′S, 116°40′E, 1980, *E. A. Griffin* (PER001630); Albany-Borden off Chillinup Rd, 34°20′S, 118°12′E, on *Melaleuca* sp., 1970, *N. Sammy*; Lake Biddy, near Lake Grace, 33°00′S, 118°56′E, on tree, 1976, *A. C. Smith* (N. Sammy); Gairdner R., 34°14′S, 119°17′E, on *Hakea* sp., 1980, *D. Richardson* (PER000941); Cape Arid Nat. Park, 34°02′S, 123°09′E, on *Hakea clovata*, 1971, *R. D. Royce* (PER000428). **Tasmania**: Rocky Cape, 40°53′S, 145°30′E, on quartzite rock, 1980, *GK* 743/80; Ansons Bay Nth, 41°02′S, 148°16′E, on *Banksia* sp., 1975, *GB* (H032680); Moores Hill, Beaconsfield, 41°13′S, 146°45′E, on *Acacia dealbata*, 1980, *GK* 216/80; Buckland, Pitts Hill, 42°36′S, 147°43′E, on *Bursaris spinosa*, 1980, *GK* 450/80; Hobart, Gunners Quoin, 42°54′S, 147°19′E, on dolerite rock, 1980, *GK* 600/80.

16. *Ramalina fissa* (Müll. Arg.) Vainio Plate 10, fig. 8.

in *Mem. Herb. Boissier* **5**: 2 (1900).

Ramalina inflata var. *fissa* Müll. Arg. in *Flora, Jena* **71**: 203 (1888). Type: Australia, King Island, Bass Strait, 1888, *French* s.n. (G! – holotype; salazinic acid and usnic acid). Plate 14, fig. 4.

Ramalina brevis var. *brevissima* F. Wilson in *Pap. Proc. R. Soc. Tasm.* **1892**: 159 (1893). Type: Australia, Tasmania, Ulverstone, Antill Ponds, *Weymouth* s.n. (not located). – *Ramalina fraxinea* var. *brevissima* (F. Wilson) Zahlbr., *Cat. Lich. Univ.* **6**: 486 (1930).

Thallus corticolous and saxicolous, greenish-grey, erect, rigid to flaccid, inflated and shrubby or flattened and almost foliose, 1–3 cm high; branching from the base only; branches variable in width, often bursting open to reveal the medulla, giving a false effect of gross inflation, with flattening of the thallus the areas directly below the apothecia remain the only part of the thallus with a central cavity; perforations when present, large, round to elongate, splitting to reveal the medulla; medulla loosely woven, sparse, adhering in patches to the inner cortex wall, the wall often marked with reticulate strands of chondroid tissue; sometimes pseudocyphellate; holdfast delimited; soralia absent.

Apothecia numerous, terminal, not spurred; sometimes laminal; disc 2–5(–8) mm diam., initially concave becoming flat; margin entire, inrolled; spores ellipsoid, mainly curved, some straight, (10–)12–16 × 4–5(–6) μm.

Chemistry. Salazinic acid and usnic acid.

Remarks. Ramalina brevis var. *brevissima* F. Wilson has been placed in the synonymy. Although the type material was not located (it is possibly lost), other specimens identified by Wilson as *R. brevis* var. *brevissima* contain salazinic acid and are small caespitose morphotypes of *R. fissa*.

Wilson identified large coarse morphotypes of this taxon as *R. fraxinea* f. *platyna* Nyl. Material held at G under the latter name consists of two thalli which contain divaricatic acid and one which contains salazinic acid. Magnusson examined these specimens and found different colour reactions, K− (divaricatic acid), and K + y (salazinic acid). These specimens have been found to belong to *R. inflata* subsp. *australis* and *R. fissa*.

Ramalina subpusilla comes near to *R. fissa* because of its similar chemistry, but morphologically it differs by producing spurred apothecia, a characteristic not found in the latter taxon. *Ramalina calcarata* Krog & Swinscow contains divaricatic acid and small amounts of salazinic acid in the hymenium; Krog & Swinscow (1974) compared it to *R. fissa* because of the reticulate-fibrose underside of both and the straight to reniform spores produced by both, but the absence of spurred apothecia in the latter taxon separates the two. Galloway (1985) recorded that *R. geniculata* (a New Zealand species often confused with *R. inflata*) contains sekikaic and salazinic (tr.) acids; but the type material (held at FH) contains divaricatic acid. Such variation in acid content of a single species adds weight to the suggestion that in Australia there is an evolutionary relationship between the depside taxon *R. inflata* subsp. *australis* and the depsidone taxon *R. fissa*, especially as similarities in morphology are also found in some specimens. However, as no Australian material was found to contain both depside and depsidone chemistry, *R. fissa* is regarded as a distinct, endemic species.

Distribution and habitat. The distribution range of *R. fissa* (Fig. 23) lies within the larger range of the two chemical races of *R. inflata* subsp. *australis* in the temperate region of Australia. It is mostly coastal in occurrence, occupying sections of the coastline in both Tasmania and the mainland not usually occupied by *R. inflata* subsp. *australis* (divaricatic acid race). In western Victoria and South Australia the inland locations of *R. fissa* are mainly different from the sites occupied by *R. inflata* subsp. *australis* (Figs 22, 23).

Variation in morphology appears to be ecophenotypic; in some coastal habitats extreme flattening of the thallus occurs, producing a dorsi-ventral form resembling a parmeloid thallus. In the dry inland regions of southern Australia the thalli are inflated, small, and very coarsely textured. On the islands of Bass Strait and Kangaroo Island, the thalli produce inflated pustules or small branchlets on the surface. A lower 'pseudo-cortex' is often produced to cover the exposed medulla in some thalli with completely split-open branches.

Occasionally *R. fissa* occurs on rocks and produces a much reduced growth form. On Hunter Island, Bass Strait, specimens grow on quartzite; Tasmanian collections from Cape Deslacs and Bruny Island do not record the rock type. Some of these saxicolous specimens are tiny, single, balloon-shaped thalli which closely resemble thalli of *R. inflata* subsp. *australis* (divaricatic acid race) collected off fine twigs of *Leptospermum* sp. in Western Australia. Usually *R. fissa* is corticolous, occurring on a number of different tree species (*Acacia* spp., *Leucopogon parviflora, Leptospermum laevigatum, Pimelea serpyllifolia*, and *Melaleuca lanceolata*); it occurs on the mangrove *Avicennia marina* and has been found growing on fence posts at Marlo, Victoria. It does not show any substrate preference.

World distribution. Australia.

Victoria: Linga, 13 km N of, Pink Lakes, 35°06′S, 141°40′E, on dead wood, 1970, *GB & JC* (H032663); Casterton, 51·5 km N of, 37°20′S, 141°20′E, on *Acacia* sp., 1973, *RF* (MEL1036009); Creswick, 37°26′S, 143°54′E, on *Pinus* sp., 1963, *J. H. Willis* (MEL9335); Lake Burrumbeet, 37°28′S, 143°40′E, on *Pinus* sp., 1945, *P. Bibby* (MEL10018); Marlo, 37°48′S, 148°42′E, on fence post, 1978, *JAE* (JAE5195); Troidea Hill, 37°57′S, 141°19′E, on *Banksia* sp., 1965, *RF* (MEL1026193); Portsea, 38°20′S, 144°42′E, on shrub, 1964, *J. Williams* (MEL1516513); Portland, 38°21′S, 141°36′E, on *Malus* sp., 1965, *RF* (MEL1516516); Western Port Bay, 38°26′S, 145°08′E, on *Avicennia marina*, 1978, *GNS* (BRIU2347NS); Wilsons Prom. N of, 39°05′S, 146°25′E, on *Acacia* sp., 1980, *GNS* (BRIU3198NS). **Bass Strait**: Hogans I, 39°13′S, 146°59′E, on *Leucopogon* sp., 1973, *JW* (MEL10130013); Little Dog I,

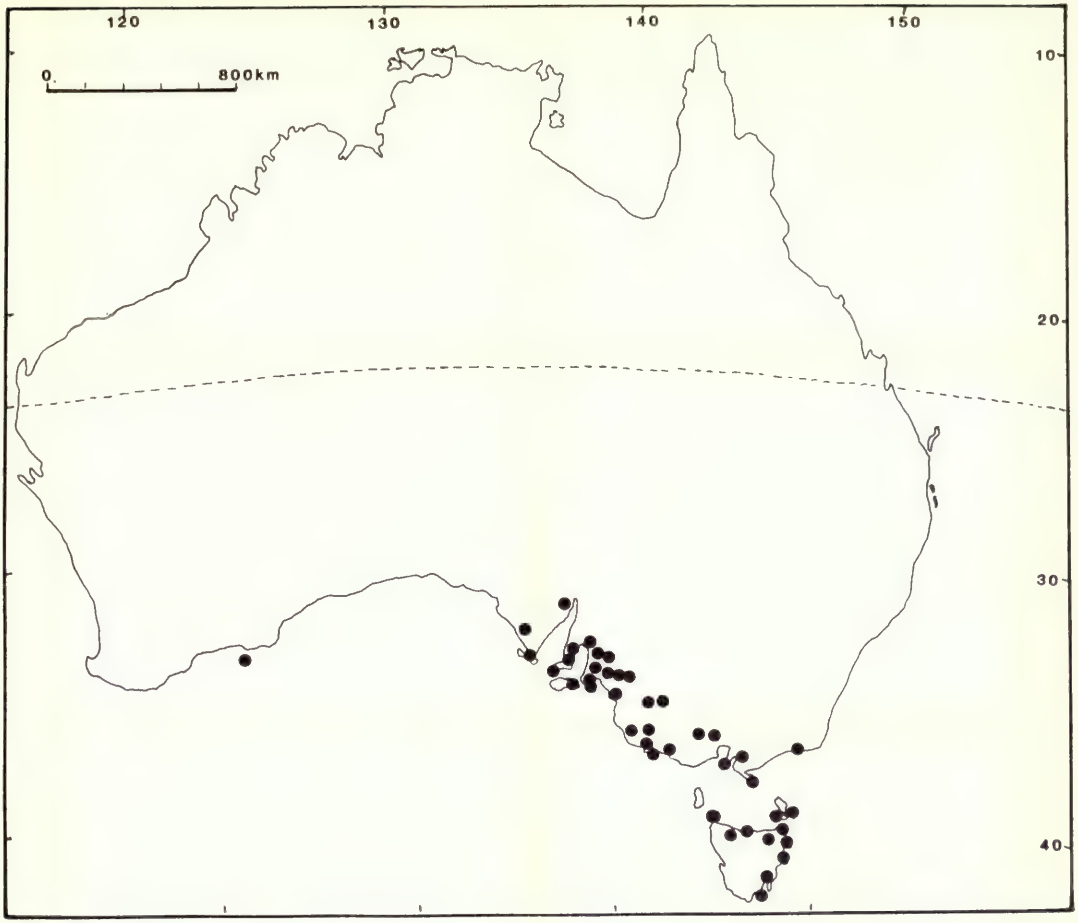


Fig. 23 Distribution of *R. fissa*.

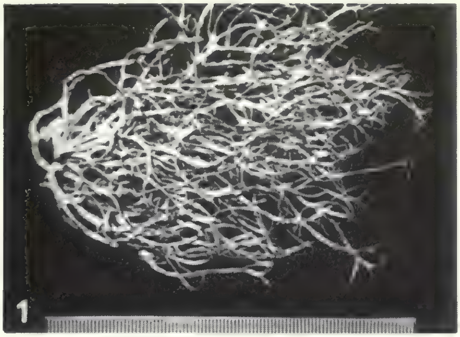
40°15′S, 148°17′E, on twigs, 1977, *JW* (MEL1026160); Flinders I, 40°01′S, 148°02′E, on *Leptospermum laevigatum*, 1969, *JW* (MEL1019938); Hunter I, 40°31′S, 144°45′E, on quartzite, 1973, *T. V. Muir* (MEL1021245). **Tasmania**: Table Cape, 40°57′S, 145°43′E, on *Acacia melanoxylon,* 1970, *GB* (HO32296); Eddystone Beach, 40°59′S, 148°19′E, on dead tree, 1973, *GB* (H032679); Devonport, 41°11′S, 146°21′E, on *Acacia* sp., 1980, *GNS* (BRIU3240NS); Chain of Lagoons R., 41°39′S, 148°18′E, on bush, 1973, *GB* & *JC* (H032667); Cape Deslacs, 42°57′S, 147°33′E, on rock, 1965, *GB* & *JC* (H032647); Bruny I, Isthmus Bay, 43°23′S, 147°17′E, on tree, 1982, *AA* (BRIU3707NS). **South Australia**: Lock, 25 km WSW of, 33°40′S, 135°20′E, 1967, *N. N. Donner* (AD97648157); Yararoo Gorge, 34°20′S, 138°20′E, 1967, *B. Copley* (AD97419099); Kangaroo I, 35°40′S, 137°38′E, on Mallee bush, 1971, *G. Jackson* (AD97410372); Coorong, 36°12′S, 139°40′E, 1965, *A. C. Beauglehole* (MEL1020684); Naracoorte, 36°58′S, 140°45′E, on dead wood, 1973, *M. Beck* (H32559); Eyre Peninsula, Cape Catastrophe, 34°40′S, 135°50′E, on *Melaleuca* sp., 1970, *RF* (MEL1020693).

17. ***Ramalina nervulosa*** (Müll. Arg.) des Abb.

in *Bull. Inst. fr. Afr. noire* **14**: 25 (1952).
Ramalina farinacea var. *nervulosa* Müll. Arg. in *Flora, Jena* **66**: 21 (1883). Type: Australia, Queensland, Daintree River, Pentzke s.n. (G! – lectotype; divaricatic acid, stenosporic acid, and usnic acid).

var. ***nervulosa*** Plate 11, fig. 3; Plate 14, fig. 7.

Thallus corticolous, pale green to stramineous, subpendulous to pendulous, usually 4–10 cm long, exceptionally to 30 cm; branching sparse with unequal dichotomy producing long attenuate branches, often tangled about one another; branch width (0·3–)1·0–1·5(–2·0) mm,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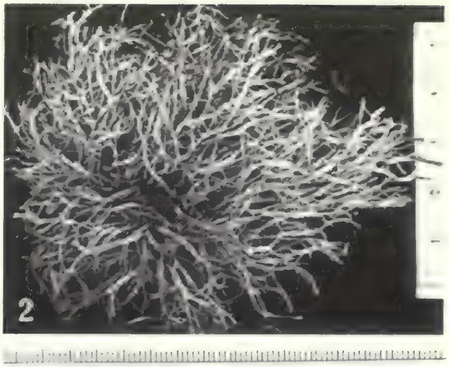
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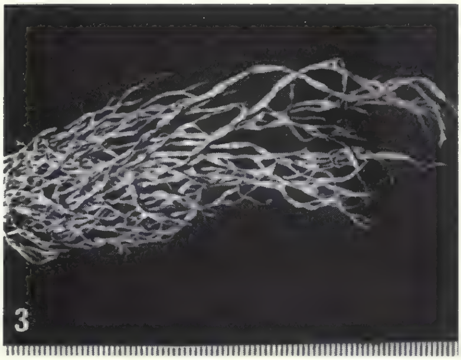
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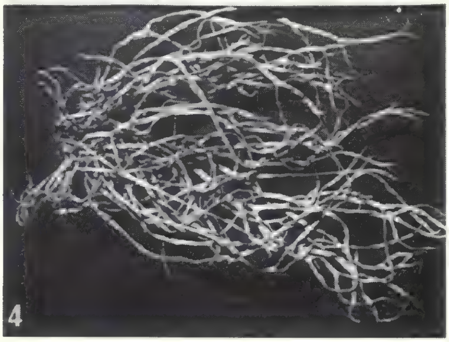
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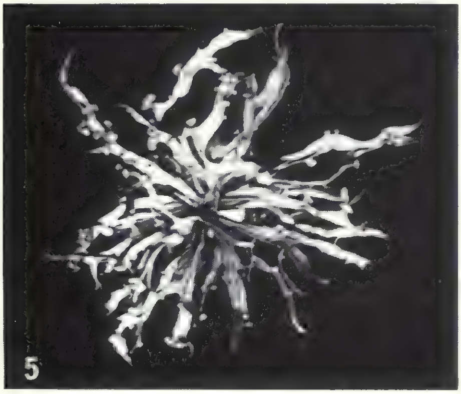
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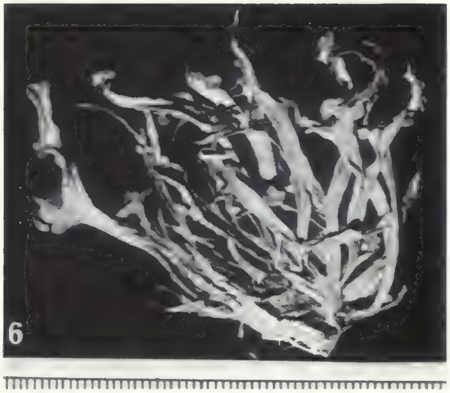
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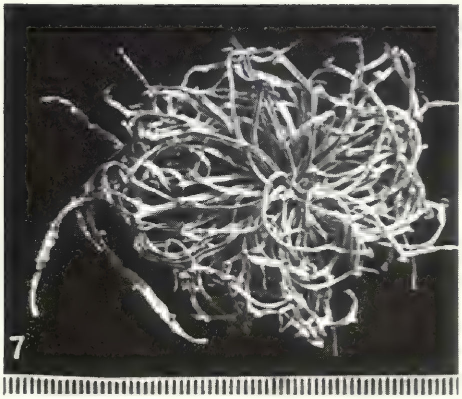
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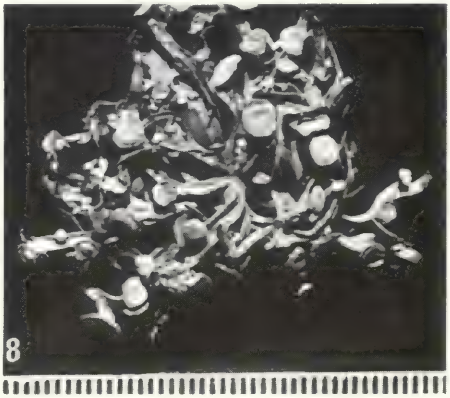
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branches flat and narrow, when extremely narrow becoming subterete and twisted or undulate along the entire length, branches occasionally fuse; cortex matt, marked with longitudinal pseudocyphellae which cause the 'nervulose' appearance of this species; several branches arise from a well defined holdfast; soralia marginal, round to ellipsoid. Apothecia not seen.

Chemistry. Divaricatic acid and stenosporic acid and usnic acid.

Remarks. Müller [Arg.] (1883) applied the name *R. farinacea* var. *nervulosa* to specimens which had been sent to him from Norfolk Island, Australia, Tahiti, the Marianas, and India which closely resembled *R. farinacea*. Des Abbayes (1952) collected and examined sorediate specimens from the Ivory Coast (West Africa) and thought they belonged to the same species that Müller had described, but he believed that they were sufficiently distinct from *R. farinacea* to warrant species rank as *R. nervulosa* (Müll. Arg.) des Abb. (Stevens, 1983*a*).

When the five specimens held at G in the Müller [Arg.] herbarium were examined, it was found that, although their morphology was similar in some instances, each had a quite different chemistry and belonged to separate taxa. The majority of the thalli bear the 'nervulose markings' (linear pseudocyphellae and longitudinal cracks) which caused the name 'nervulosa' to be applied to them; this trait is quite distinctive as remarked upon by des Abbayes. Of the five specimens cited by Müller (1883) only the Australian material from Daintree River Queensland contains divaricatic acid and stenosporic acid. This specimen was designated as lectotype by Filson in 1971.

Distribution and habitat. Ramalina nervulosa var. *nervulosa* occurs along the Queensland coastline from latitude 14°–28°S (Fig. 24), and at several inland locations (Stewart River (14°S), Barrow's Range (15°S), and Atherton Tableland (17°S)). This taxon is sympatric with its variety (var. *luciae*) for much of its distribution in Australia. The largest specimens collected, which exceed 20 cm, grew at Stewart River (14°S) and Turkey (24°S), the reason for such exceptional growth is not known. The mangroves *Ceriops tagal* and *Rhizophora stylosa* are the usual phorophytes for this taxon.

World distribution: Burma/Bangladesh, Indonesia (Java and Bali), South Africa, and Australia.

Queensland: Stewart R., 14°05′S, 143°38′E, 1900, *Johnston* (MEL 4443); Barrons Range, 15°36′S, 145°04′E, on shrub, 1983, *M. Godwin* (C2436); Mossman Rifle Range, 16°20′S, 145°45′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4128NS); Trinity Inlet (Cairns); 16°56′S, 145°46′E, on *Ceriops tagal*, 1976, *D. Tarte* (BRIU2589NS); Hinchinbrook I, 18°17′S, 146°13′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3131NS); Eimeo, 21°09′S, 149°09′E, on *Rhizophora* sp., 1976, *GNS* (BRIU3544NS); St Lawrence, 22°21′S, 149°32′E, on *Excoecaria agallocha*, 1976, *NCS* (BRIU2131NS); Port Alma, 23°35′S, 150°51′E, on *Rhizophora stylosa*, 1975, *RWR* (BRIU698RR); Gladstone, 23°50′S, 151°16′E, on *Rhizophora stylosa*, 1980, *GNS* (BRIU3348NS); Rodds Peninsula, 24°02′S, 151°40′E, on *Ceriops tagal*, 1975, *GNS* (BRIU1292NS); South Stradbroke I, 27°55′S, 153°30′E, on *Ceriops tagal*, 1975, *H. T. Clifford* (BRIU76RR).

var. **dumeticola** (Krog & Swinscow) N. Stevens Plate 11, fig. 2.

in *Lichenologist* **15**: 228 (1983).

Ramalina dumeticola Krog & Swinscow in *Norw. J. Bot.* **23**: 163 (1976). Type: Kenya, Coast Province, Kwale District, *Krog* 3K30/127 (O! – holotype, BM! – isotype; homosekikaic acid (M), sekikaic acid (M), 4'-0-methylnorhomosekikaic acid (M), ramalinolic (t), 4'-0-demethylsekikaic acid (t), 4'-0-methylnorsekikaic acid (t) and usnic acid).

Thallus corticolous, pale green to yellow-green, tufty, subpendulous, 4–6 cm long; branching dichotomous, moderate to dense but never intricately branched; branch width (0·2)0·5–1·0(–

◀ **Plate 11** Thallus growth forms in the Australian Ramalinae. Scale in mm. Fig. 1 *R. pacifica*. Fig. 2 *R. nervulosa* var. *dumeticola*. Fig. 3 *R. nervulosa* var. *nervulosa*. Fig. 4 *R. nervulosa* var. *luciae*. Fig. 5 *R. subfraxinea* var. *confirmata*. Fig. 6 *R. subfraxinea* var. *leiodea*. Fig. 7 *R. subfraxinea* var. *subfraxinea* (narrow form). Fig. 8 *R. subfraxinea* var. *norstictica* (type specimen).

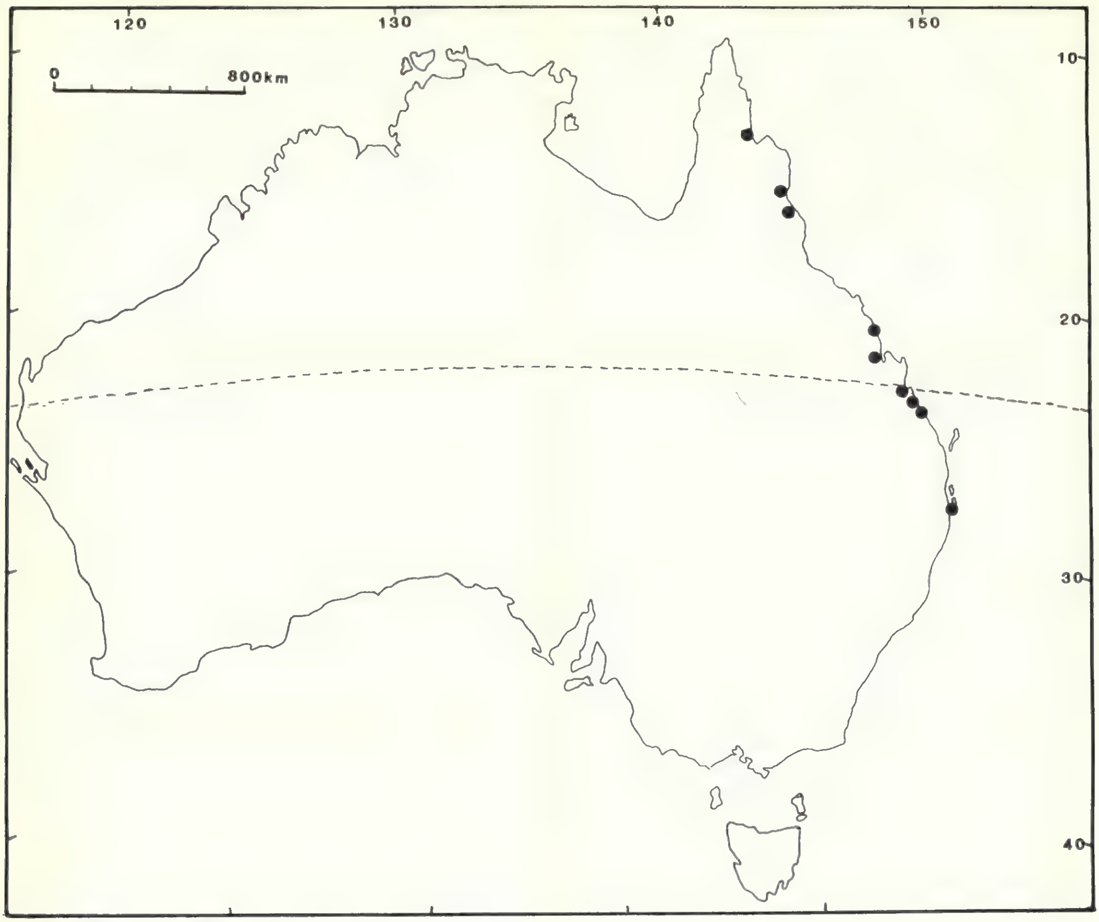


Fig. 24 Distribution of *R. nervulosa* var. *nervulosa*.

2·0) mm, branches compressed, flat, usually canaliculate for part of their length, some branches subterete distally, apices attenuate, forked or broken off and appearing blunt; surface matt or shiny, smooth, faint pseudocyphellae sometimes present; holdfast delimited; soralia marginal, round, ellipsoid or elongate. Apothecia not seen.

Chemistry. Homosekikaic acid (M), sekikaic acid (M), 4'-0-methylnorhomosekikaic acid (m), 4'-0-demethylsekikaic acid (t), ramalinolic acid (t), 4'-0-methylnorsekikaic acid (t) [the last two acids are rarely detected with tlc] and usnic acid.

Remarks. Initially the Australian material of this taxon was thought to be a morphotype of *R. peruviana* as the two are sympatric in occurrence. However, the shape of the soralia and branching pattern of the two sets them apart. The morphology of *R. nervulosa* var. *dumeticola* closely resembles that of *R. farinacea*. Although both *R. peruviana* and *R. nervulosa* var. *dumeticola* contain acids in the sekikaic aggregate, the presence of 4'-0-methylnorhomosekikaic acid as a minor metabolite in the latter taxon and not in the former, and the constant occurrence of ramalinolic acid in *R. peruviana* but not in *R. nervulosa* var. *dumeticola* distinguishes the two on chemical grounds.

Distribution and habitat. The occurrence of *R. nervulosa* var. *dumeticola* in Australia at subtropical latitudes appears to be an anomaly (Fig. 25). Previous research (Stevens, 1983*a*) has shown its distribution to be mostly equatorial and northern hemisphere tropical (to latitude 15°N), penetrating to latitude 8°S (based on known collections). Its presence in the mountains of

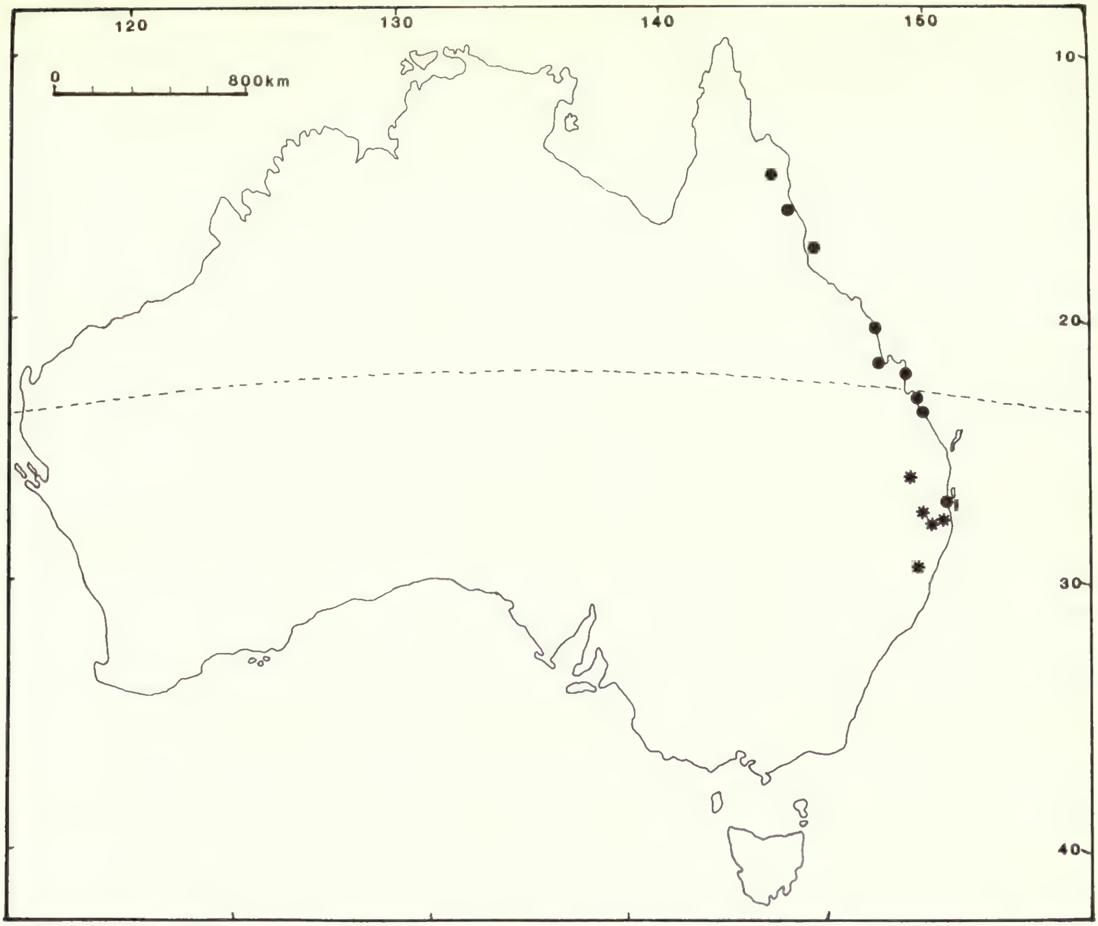


Fig. 25 Distribution of *R. nervulosa* var. *luciae* ● and var. *dumeticola* ★.

New Guinea at latitude 6°S (established during this present research) is in accord with this distribution pattern. The subtropical occurrence of this taxon in Australia in the mountain areas between latitudes 26°S–30°S cannot be explained, nor can the complete absence of this taxon from any coastal habitats.

World distribution. India, Indonesia (Java), Philippines, Marianas Is, Kenya, Ivory Coast, Príncipe, Ascension, and Australia.

Queensland: Bunya Mts, 26°50′S, 151°40′E, on understorey shrub, 1979, *GNS* (BRIU2971NS); Mt Castle, 2 km SW of, 27°58′S, 152°23′E, on rainforest twig, 1983, *NCS* (BRIU3677NS); Cunninghams Gap, Mt Cordeaux track, 28°03′S, 152°23′E, on rain-forest twig, 1979, *GNS* (BRIU3697NS); The Head, Moss Gardens, 28°15′S, 152°30′E, on twigs of rain-forest shrub, 1981, *GNS* (BRIU3622NS); O'Reillys, Botanical Walk, 28°15′S, 153°08′E, on rain-forest shrub, 1983, *GNS* (BRIU3731NS); Gamboobal State Forest, 28°14′S, 152°20′E, on dead tree on mountain top, 1983, *GNS* (BRIU3737NS); Queen Marys Falls, 5 km N of, 28°20′S, 152°22′E, on rain-forest tree, 1983, *GNS* (BRIU3736NS). **New South Wales**: Chaelundi Mt, 37 km N of Ebor, 30°04′S, 152°21′E, *Acacia orrites*, 1978, *D. Verdon* (CBG7809394); Cattle Ck State Forest, 12 km NNE of Dorrigo, 30°15′S, 152°03′E, on *Banksia integrifolia*, 1978, *D. Verdon* (CBG8203532).

var. ***luciae*** (Molho et al.) N. Stevens Plate 11, fig. 4.

in *Lichenologist* **15**: 227 (1983).
Ramalina luciae Molho, Bodo, Culb. & C. Culb. in *Bryologist* **84**: 396 (1981). Type: Fiji, Kambara (=

Kabara) Island, *Salvat* B. 358a (DUKE – holotype; 'sekikaic, homosekikaic, 4'-0-demethylsekikaic and 4'-0-methylnorsekikaic acids and usnic acid').

Thallus corticolous, pale green to stramineous, subpendulous to pendulous, up to 7 cm long, exceptionally to 18 cm; branching sparsely dichotomous, producing extreme elongation between dichotomies; branch width (0·3)0·5–1·0(–2·0) mm, branches flattened at the base but subterete to terete towards the apices, slightly twisted along the whole length, fusion between branches common, causing a tangled growth form; cortex matt to shiny; longitudinal pseudocyphellae usually present but rarely becoming laminal soralia; simple cracks in the cortex and splitting along the margin occurs; several basal branches arise from a well defined holdfast.

Apothecia rare, lateral, disc 2 mm diam, concave to ellipsoid to fusiform, sometimes appearing 3,4-celled; straight or rarely slightly curved (10–)12–16(–18) × 4–5(–6) μm.

Chemistry. Sekikaic acid (M), 4'-0-methylnorsekikaic acid (m), 4'-0-demethylsekikaic acid (m or t), homosekikaic acid (t), ramalinolic acid (t), 4'-0-methylnorhomosekikaic acid (t).

Remarks. Ramalina nervulosa var. *luciae* was described by Molho, Bodo, Culberson & C. Culberson (1981) from a specimen collected in Fiji. Similar material held at G as a syntype of *R. farinacea* var. *nervulosa* Müll. Arg., was collected from Tahiti last century by Jardin. This taxon is a common maritime *Ramalina* along the eastern coastline of tropical Australia.

Because of the similarity in morphology between *R. nervulosa* var. *nervulosa* and *R. nervulosa* var. *luciae*, chemical differences had to be used as the main criteria to separate them. The rank of variety was given to each taxon in accordance with the guidelines set out by Hawksworth (1976). Apart from chemical difference, their distribution range when considered on a global scale shows two distinct patterns (Stevens, 1983*a*).

The chemistry of two sorediate *Ramalina* species resembles that of *R. nervulosa* var. *luciae* (viz. *R. peruviana* Ach. and *R. intermediella* Vainio) but both of these have a distinct morphology which distinguishes them from the morphology of *R. nervulosa* var. *luciae*.

Distribution and habitat. The distribution of *R. nervulosa* var. *luciae* (Fig. 25) covers a coastal region from approximately latitudes 15°–27°S in Queensland. For most of its range this taxon is sympatric with both *R. nervulosa* var. *nervulosa* and *R. pacifica*.

The majority of the collections was made at sea-level from mangrove communities, the main phorophytes being *Ceriops tagal*, and to a lesser extent *Avicennia marina* and *Rhizophora stylosa* which grow on the sheltered, landward fringe of the mangroves. The most northerly collections in Australia are from inland sites, e.g. Butchers Hill, Lakeland, latitude 15°52′S, and Atherton Tableland, latitude 17°16′S. Both of these sites are approximately 45 km from the coast at an altitude of 900 m, indicating cooler habitat requirements at lower latitudes; a tendency observed in the other members of the tropical *R. farinacea* complex (Stevens, 1983*a*).

At latitude 21°S (Eimeo Beach, Mackay) this species grows prolifically on the landward fringe of *Rhizophora stylosa* communities; in this habitat fertile specimens as well as very long specimens occur.

World distribution. Sri Lanka, Indonesia (Celebes), Kenya, Australia, New Hebrides, Fiji, Cook Is, and Tahiti.

Queensland: Lakeland, Butchers Hill, 15°52′S, 144°55′E, on rain-forest shrub, 1983, *GNS* (BRIU4108NS); Mossman, 16°20′S, 145°24′E, on *Pinus* sp. in garden, 1983, *C. McCracken* (BRIU4241NS); Yungaburra Rd Atherton, 17°16′S, 145°29′E, on *Casuarina* sp., 1983, *HS* (CBG8302450); Hinchinbrook I, 18°17′S, 146°13′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3137NS); Eimeo, 21°09′S, 149°09′E, on *Rhizophora stylosa*, 1976, *GNS* (BRIU3542NS); St Lawrence, 22°21′S, 149°32′E, on *Ceriops tagal*, 1980, *GNS* (BRIU3600NS); Corio Bay, 22°58′S, 150°46′E, on *Ceriops tagal*, 1974, *D. Tarte* (BRIU1168NS); Gladstone, 23°50′S, 151°16′E, on *Ceriops tagal*, 1980, *GNS* (BRIU3566NS); Tannum Sands, 23°57′S, 151°16′E, on *Ceriops tagal*, 1975, *RWR* (BRIU833RR); Turkey, 24°06′S, 151°40′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU280NS); Toogoom, 25°15′S, 152°40′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4149NS); Serpentine Ck, 27°23′S, 151°39′E, on *Ceriops tagal*, 1975, *GNS* (BRIU1044NS).

18. *Ramalina pacifica* Asah. Plate 11, fig. 1; Plate 14, fig. 8.

in *J. Jap. Bot.* **15**: 213 (1939). Type: Micronesia, Marianas, Saipan Island, 1925, *Kimura* s.n. (TNS! – lectotype; salazinic acid and usnic acid).

Ramalina insularum Magnusson in *Ark Bot.* **3** (10): 361 (1956). Type: Fiji Is., 1862, *Daemel* s.n. (H! – lectotype; salazinic acid and usnic acid).

Thallus corticolous, rarely saxicolous, grey-green, tufty, subpendulous to pendulous, 4–8 cm long, exceptionally to 32 cm; branching dichotomous, sparse to moderately dense but extremely variable; branch width (0·5–)1–4 mm, branches compressed, flat, some splitting along the margins; broad in the basal region but gradually narrowing towards the apices or narrow in the basal region and continuing the same width to the apices; apices attenuate, mostly forked; cortex matt or shiny, smooth or with linear pseudocyphellae slightly or strongly developed; holdfast delimited; soralia marginal and laminal, round to ellipsoid (Plate 1, fig. 3), often coalescing, the edges revolute.

Apothecia rare, marginal, disc 1–3 mm diam., concave, plane to convex, with edges sometimes incised at maturity; spores fusiform or ellipsoid, (Plate 4, fig. 3), straight or very slightly curved, 12–16(–20) × 4–6 μm.

Chemistry. Salazinic acid ± protocetraric acid and usnic acid.

Remarks. The name *Ramalina pacifica* was given to sorediate material found on the Saipan Islands (Marianas) and on Hachijo Island (Japan) by Asahina (1939); he stated that lichenologists had identified his species as various varieties of *R. farinacea.* Asahina also commented that some thalli of *R. pacifica* contained both salazinic and sekikaic acids. It appears that the sekikaic acid he observed could have come from a contaminant, perhaps *R. intermediella* or *R. nervulosa* var. *dumeticola*, as both of these species are maritime and grow in association with *R. pacifica*.

Stevens (1983*a*) placed *R. pacifica* in the tropical-subtropical group of the *R. farinacea* complex. It is the only taxon in this group which has a depsidone chemistry. In ancient times it may have been contiguous with the protocetraric acid species of *R. farinacea* found on Macquarie I. (latitude 55°S), but the links are now broken except for the presence of trace amounts of protocetraric acid in some specimens of *R. pacifica*.

Ramalina insularum Magnusson, a synonym of *R. pacifica*, was collected from Fiji. Its morphology more closely resembles that of *R. nervulosa* var. *luciae* material collected from Fiji than it does the Australian *R. pacifica*, which illustrates the phenomenon of convergent morphology of these two Fijian specimens which are sympatric.

Distribution and habitat. The distribution range of *R. pacifica* covers an area which is mainly subtropical to warm temperate (Fig. 26), although several collections have been made in tropical Australia, e.g. Hinchinbrook I. (latitude 18°S) and Shute Harbour (latitude 20°S). In these areas the rainfall exceeds 2000 mm p.a. and the thalli are very narrow and delicate with smooth, shiny surfaces, without pseudocyphellae. Collections from the drier latitudes along the Queensland coast (latitudes 22°–24°S which receive 800–1100 mm p.a.) comprise thalli which produce numerous pseudocyphellae along the whole length of the branches; these thalli are generally broader than the thalli from the higher rainfall habitats. Only one inland collection of *R. pacifica* was made, at Atherton Tableland.

The main phorophytes for this taxon are the mangroves *Ceriops tagal* and *Avicennia marina. Ramalina pacifica* attains its maximum growth at latitudes 27°–28°S (Moreton Bay), annual rainfall 1100–1500 mm p.a. In two relatively undisturbed well-established communities of *Avicennia marina* some exceptional specimens 32 cm long with branches 2–3 mm wide were found. Fertile specimens also occurred in this environment. The majority of the thalli produced pseudocyphellae as well as both marginal and laminal soralia. In areas of Moreton Bay where *R. pacifica* grew on *Ceriops tagal*, the thalli were small (up to 5 cm long) with narrow branches (to 1·0 mm wide), and had a smooth cortex which lacked pseudocyphellae or produced them at the base of the branches only.

From latitude 28°S to the limit of *R. pacifica* distribution at 35°S, this taxon occurs on

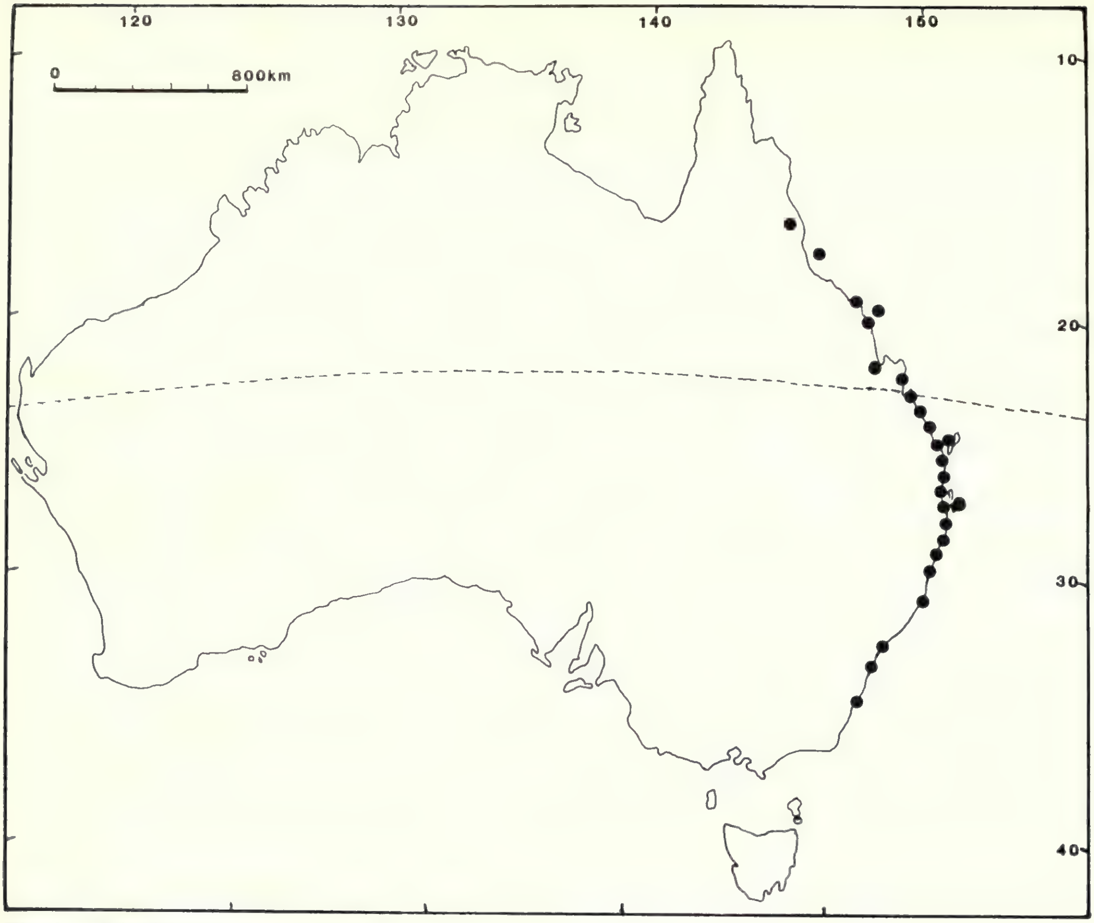


Fig. 26 Distribution of *R. pacifica*.

Avicennia marina (*Ceriops tagal* does not extend beyond latitude 28°S). Pseudocyphellae are usually present on the branches which reach 8 cm in length with a maximum width of 2 mm. The annual rainfall in this section of coastline is between 1000–1500 mm p.a.

It was not able to be established whether the amount of rainfall or the type of substrate had the greater influence on the variation in morphology of this taxon.

Ramalina pacifica is rarely saxicolous but occurs on rock at Norries Head, New South Wales, in association with *R. subfraxinea* var. *confirmata*, another taxon which is usually corticolous. Presumably the rocks in this area of coastline are able to produce a microhabitat which is equivalent to that found in tree communities on other parts of the coast, enabling both taxa to become established on the cliff face.

World distribution. Burma/Bangladesh, Japan, Indonesia (Java), Marianas Is, South Africa, Australia, New Hebrides, New Zealand, and Cook Is.

Queensland: Tinaroo Dam, 17°15′S, 145°36′E, on *Plumeria* sp., 1983, *GNS* (BRIU41NS); Hinchinbrook I, 18°17′S, 146°13′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3441NS); Bowen, 19°59′S, 148°22′E, on *Lumnitzera racemosa*, 1979, *GNS* (BRIU3284NS); Shute Harbour, 20°16′S, 148°47′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3283NS); Brampton I, 20°49′S, 149°18′E, *J. M. Gilbert* (H032317); Eimeo, 21°09′S, 149°09′E, on *Rhizophora stylosa*, 1976, *GNS* (BRIU1369NS); St Lawrence, 22°21′S, 149°32′E, on *Excoecaria agallocha*, 1976, *GNS* (BRIU2127NS); Keppel Sands, 23°21′S, 150°47′E, on *Excoecaria agallocha*, 1975, *RWR* (BRIU779RR); Port Alma, 23°35′S, 150°51′E, on *Rhizophora* sp., 1975, *RWR* (BRIU699RR); Gladstone, 23°50′S, 151°16′E, on *Rhizophora stylosa*, 1980, *GNS* (BRIU3570NS); Tannum Sands, 23°57′S, 151°16′E, on *Rhizophora stylosa*, 1980, *GNS* (BRIU3599NS); Turkey, 24°06′S, 151°37′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1266NS); Rodds Peninsula, 24°02′S, 151°40′E, on *Ceriops tagal*, 1975, *GNS* (BRIU1153NS); Round Hill Hd., 24°10′S, 151°54′E, on *Rhizophora stylosa*, 1975, *RWR* (BRIU915RR); Fraser I, Wathumba Ck, 24°59′S, 152°55′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU3597NS); Burrum Hds, 25°10′S, 152°35′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1129NS); Urangan Beach, 25°19′S, 152°55′E, on *Callitris columellaris*, 1978, *GNS* (BRIU2841NS); Tin Can Bay, 25°55′S, 153°00′E, *GB* (H032319); Noosa Hds, 26°24′S, 152°07′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1807NS); Deception Bay, 27°10′S, 153°02′E, on *Avicennia marina*, 1978, *GNS* (BRIU2561NS); Tingalpa Ck, 27°28′S, 153°11′E, on *Avicennia marina* 1977, *GNS* (BRIU1756NS); Coochiemudlo I, 27°35′S, 153°20′E, on *Rhizophora stylosa*, 1977, *GNS* (BRIU1654NS); Little Rocky Pt, 27°38′S, 153°18′E, on *Ceriops tagal*, 1977, *GNS* (BRIU1438NS); Stradbroke I, Swan Bay, 27°45′S, 153°26′E, on *Ceriops tagal*, *H. T. Clifford* (BRIU3075RR). **New South Wales**: Brunswick Hds, 28°32′S, 153°32′E, on *Callitris* sp., 1980, *GNS* (BRIU3486NS); Yamba, 29°27′S, 153°20′E, on *Avicennia marina*, 1977, *GNS* (BRIU2220NS); Boambee Ck, 30°22′S, 153°05′E, on *Avicennia marina*, 1977, *GNS* (BRIU2032NS); Nambucca Hds, 30°39′S, 153°00′E, on *Avicennia marina*, 1977, *GNS* (BRIU2001NS); Port Macquarie, 31°27′S, 152°54′E, on *Avicennia marina*, 1977, *GNS* (BRIU1989NS); Patonga, 33°30′S, 151°20′E, on *Avicennia marina*, 1978, *GNS* (BRIU2308NS); Towra Pt., 34°01′S, 151°13′E, on *Avicennia marina*, 1977, *C. Scarlett* (BRIU634CS); Sussex Inlet, 35°19′S, 150°36′E, on *Avicennia marina*, 1977, *RWR* (BRIU2226NS).

19. ***Ramalina subfraxinea*** Nyl.

in *Bull. Soc. Linn. Normandie* II, **4**: 139 (1870). Type: South America, Columbia, Turbaco, Nova Granata, 1844, *Goudot* s.n. (PC! – lectotype; H! – isotype; sekikaic acid, homosekikaic acid, an unknown and usnic acid).

var. ***subfraxinea*** Plate 11, fig. 7; Plate 12, figs 3, 7; Plate 15, fig. 2.

Thallus corticolous, pale green to grey-green, erect to subpendulous, up to 3 cm long, exceptionally to 12 cm; branching subdichotomous, sparse; branch width 0·5–1·0(–3·5) mm, branches compressed, narrow and canaliculate with attenuate apices or broad and flat with blunt apices; surface matt or shiny, marginal tuberculate pseudocyphellae frequent, laminal punctiform pseudocyphellae on broad branches; holdfast delimited; soralia absent.

Apothecia sparse to numerous, marginal and subterminal; disc 1–4 mm diam., concave, plane to convex; margin entire; spores ellipsoid, straight to slightly curved, 11–12(–16) × 4–5(–6) μm.

Chemistry (Australian taxa). Sekikaic acid, homosekikaic acid, ramalinolic acid, 4'-0-demethylsekikaic acid, paludosic acid, 4'-0-methylnorsekikaic acid, and usnic acid or divaricatic acid ± faint sekikaic acid and usnic acid.

Remarks. Nylander (1870) reported material of *R. subfraxinea* from Nova Granata (Goudot), Mauritius (Gretan ex hb. Lenorm.), Bourbon I. (Boivin), and the Marianas Islands (Gaudichaud). Examination and chemical analysis of material held at H-NYL and PC revealed that the material from Nova Granata contained either the acids of the sekikaic aggregate or divaricatic acid, whereas all of the material from Mauritius, Bourbon I., and the Marianas Is. contained boninic acid. Those collections found to contain boninic acid belong to the species *R. leiodea* (Stevens, 1982), regarded as *R. subfraxinea* var. *leiodea* in the present study.

Material from Nova Granata, collected by Goudot, is held at both PC and H; the material from PC comprises several thalli in good condition on a twig, whereas the specimen held at H is small. Every thallus on the twig held at PC was analysed and the thallus herein designated as lectotype contains sekikaic acid, homosekikaic acid, and faint 4'-0-demethylsekikaic acid. The morphology of this thallus fits the description in the protologue: 'subsimilis *Ramalinae fraxineae* minori et attenuatae, sed sporis (subcurvulis) rectioribus tenuioribusque (longit 0,011–18 millim. crassit 0,0035–0,0045 millim.)'.

It was found that several thalli on the twig contain divaricatic acid, although morphologically identical to those containing sekikaic acid. The thallus containing sekikaic acid was chosen for lectotypification in preference to a thallus containing divaricatic acid because of the large number of sekikaic acid specimens found in Australia compared to the few specimens which contain divaricatic acid. Another reason for this choice was the record (Krog & Swinscow, 1976) of the presence of the sekikaic acid aggregate in both PC and H collections of *R. subfraxinea*.

Distribution and habitat. Ramalina subfraxinea var. *subfraxinea* is tropical in distribution, reaching its southern limit at latitude 24°S, on the eastern coast of Australia; on the northern coastline it has been collected from three areas (Darwin, Gunn Pt, and Gove) at latitude 12°S (Fig. 27). This taxon has two chemical races (a) a sekikaic acid aggregate race and (b) a divaricatic acid race. The former is widely distributed from 12°S–24°S, whereas the divaricatic acid race has a restricted range between latitudes 15°51′S and 18°17′S (Fig. 31), where both races are sympatric.

The occurrence of *R. subfraxinea* var. *subfraxinea* is almost entirely coastal, with only one inland collection from Butchers Hill (15°51′S) where both races occur on shrubs in a low closed-format community. Thalli from this area contain divaricatic acid + trace amounts of sekikaic acid or sekikaic acid only indicating a close affinity between the two acid races and strengthening the argument for not separating each acid as a different variety of *R. subfraxinea*.

The main phorophytes for this taxon are *Ceriops tagal, Rhizophora stylosa, Lumnitzera racemosa, Excoecaria agallocha*, and several rain-forest trees which occur along the tropical beaches.

World distribution. India?, Australia, and South America (Colombia).

Northern Territory: Darwin, Stuart Park, 12°27′S, 130°50′E, on *Ceriops tagal*, 1981, *GNS* (BRIU3496NS); Gunn Point, 12°08′S, 130°59′E, on *Lumnitzera racemosa*, 1979, *E. Hegerl* (BRIU3115NS); Gove Airport,

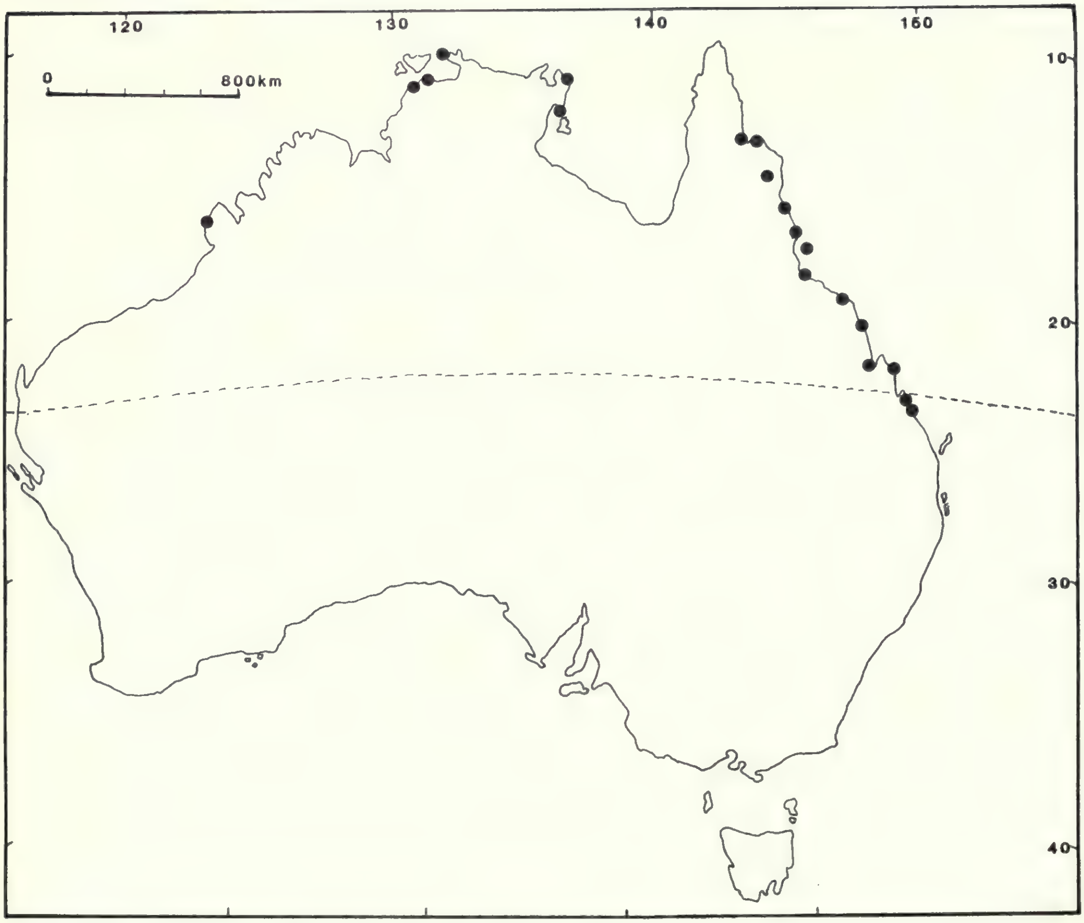


Fig. 27 Distribution of *R. subfraxinea* var. *subfraxinea*.

12°18′S, 136°50′E, on *Croton* sp., 1982, *N. Sammy* 820576. **Queensland**: Princess Charlotte Bay, Marrett R., 14°25′S, 144°09′E, on *Ceriops tagal*, 1979, *J. Davie* (BRIU2973NS); Lakeland, Butchers Hill, 15°51′S, 144°53′E, on rain-forest shrub, 1983, *G.N.* (BRIU4107NS); Daintree R. (south branch), 16°16′S, 145°25′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4136NS); Newell Beach, S Saltwater Ck 16°25′S, 145°25′E, on *Ceriops tagal*, 1983, *C. McCracken* (BRIU4234NS); Mossman Rifle Range, 16°27′S, 145°22′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4126NS); Trinity Inlet, 16°56′S, 145°45′E, on *Ceriops tagal*, 1975, *D. Tarte* (BRIU2464NS); North Mission Beach, 17°52′S, 146°06′E, on *Rhizophora* sp., 1979, *NCS* (BRIU2663NS); South Mission Beach, 17°55′S, 146°06′E, on *Ficus* sp., 1983, *GNS* (BRIU4161NS); Hinchinbrook I, The Haven, 18°18′S, 146°10′E, on *Lumnitzera* sp., 1979, *GNS* (BRIU3469NS); Townsville, 19°15′S, 146°50′E, on *Ceriops tagal*, 1975, *B. Ballment* (BRIU3119NS); Shute Harbour, 20°15′S, 148°47′E, on rain-forest tree, 1979, *GNS* (BRIU3139NS); Hallidays Bay, 20°56′S, 149°01′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4122NS); Eimeo, 21°09′S, 149°10′E, on *Rhizophora stylosa*, 1976, *GNS* (BRIU1353A.NS); St Lawrence, 22°21′S, 149°32′E, on *Excoecaria agallocha*, 1976, *GNS* (BRIU2132NS); Corio Bay, 22°58′S, 150°45′E, on *Rhizophora* sp., 1975, *D. Tarte* (BRIU1169NS); Rodds Peninsula, 24°02′S, 151°40′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1278NS); Turkey, 24°06′S, 151°37′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1150NS).

var. ***confirmata*** (Nyl.) N. Stevens, **comb. nov.**

Plate 11, fig. 5; Plate 12, figs 4, 10; Plate 15, figs 6, 8.

Ramalina fraxinea [subsp.] *confirmata* Nyl. in *Bull. Soc. linn. Normandie* II, **4**: 138 (1870). Type: Australia, Swan R., 1846, *Verreaux* s.n. (H-NYL 37423! – lectotype; cryptochlorophaeic acid and usnic acid).

Thallus corticolous, rarely saxicolous, grey-green, rigid, erect to subpendulous, up to 4 cm long, exceptionally to 11 cm; branching subdichotomous, sparse to moderate; branch width (0·5–)2–4(–10) mm, branches compressed, narrow and canaliculate to broad and flat, apices attenuate or blunt; surface smooth to rugose, short linear pseudocyphellae along branches or basally only; holdfast delimited; soralia absent.

Apothecia common, marginal and subterminal, rarely laminal, small thalli produce subterminal apothecia subtended by a spur; disc 2–3 mm diam., concave or plane; margin entire, slightly crenate, often incised at maturity; spores ellipsoid, straight or curved (8–)10–12(–14) × 4–5 μm.

Chemistry. Cryptochlorophaeic acid (M) ± paludosic acid (m), 4’-0-methylcryptochlorophaeic acid (m) and usnic acid.

Remarks. The name *R. fraxinea* subsp. *confirmata* Nyl. was given to material sent to Nylander by Verreaux, supposedly from Swan River, Western Australia. However, it is doubtful whether the specimens came from that area as Verreaux did not personally collect in Western Australia (Lamy, in litt.) and no further specimens have been found there. Material held at H-NYL, numbers 37421, 37423, all contain cryptochlorophaeic acid.

Until the present study both boninic acid and cryptochlorophaeic acid taxa were included in *R. leiodea* (Stevens, 1982); however, the policy adopted herein gives varietal status to different chemical races within a complex if the distribution patterns differ from one another. The boninic acid race therefore retains the name *R. subfraxinea* var. *leiodea* and the cryptochlorophaeic acid race has been give the name *R. subfraxinea* var. *confirmata*.

Distribution and habitat. This taxon is the most common maritime *Ramalina* along the eastern coastline of Australia, occurring from latitude 10°S (Sue I., north of Cape York) to latitude 31°S (Fig. 28).

Although mostly found along the shoreline, *R. subfraxinea* var. *confirmata* has been collected from the coastal ranges at Montville, Kenilworth, Bartle Frere, and Atherton Tableland.

In the mangrove communities it grows on *Avicennia marina* and *Rhizophora stylosa*. It has also been collected on many coastal shrubs and on *Casuarina equisetifolia* and *Callitris columellaris*, indicating it has no substrate specificity. This taxon was collected off a rock substrate at Norries Head, New South Wales, where metamorphic rocks form a sheer cliff facing

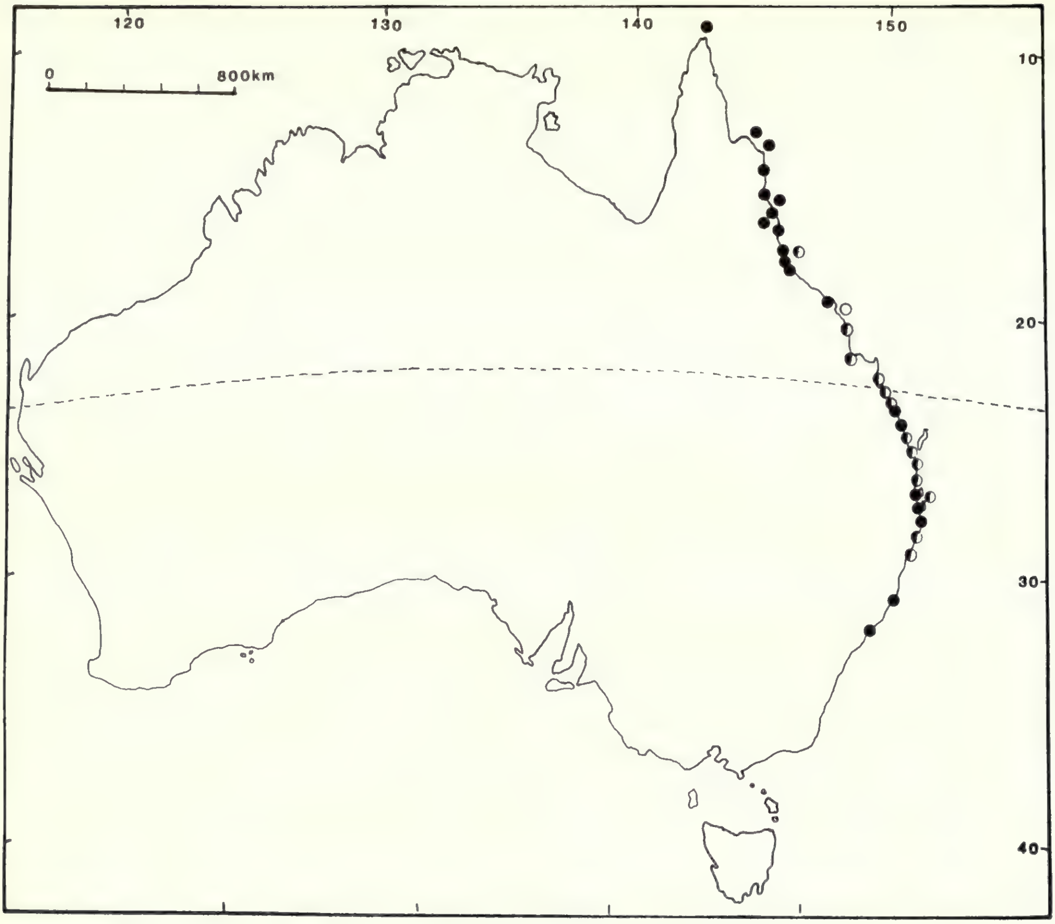


Fig. 28 Distribution of *R. subfraxinea* var. *confirmata* ● and var. *leiodea* ○.

the ocean. Such exposure is comparable with the seaward fringe of the mangroves, the position usually occupied by this taxon.

On a global scale the distribution pattern of the cryptochlorophaeic acid taxon differs from that of the boninic acid taxon. *Ramalina subfraxinea* var. *confirmata* appears to extend eastwards from Australia only as far as New Caledonia, but occurs to the north and in the Indian Ocean, whereas *R. subfraxinea* var. *leiodea* is common on most of the islands in the Pacific Ocean, as well as occurring in the Indian Ocean region.

World distribution. Timor, Zanzibar, Australia, and New Caledonia.

Queensland: Sue Island, 10°12′S, 142°49′E, on dune shrub, 1981, *J. Clarkson* 3957; Ingram I, 14°26′S, 144°50′E, on *Surina maritima*, 1984, *M. Godwin* (BRIU4282NS); Turtle Group I, 14°42′S, 145°11′E, on beach shrub, 1979, *J. Davie* (BRIU3145NS); Cooktown, 15°28′S, 145°15′E, on *Rhizophora* sp., 1983, *G.N.* (BRIU4112NS); Green Island, 16°45′S, 145°59′E, on beach shrub, 1976, *JAE* (JAE 2593); Trinity Inlet, 16°56′S, 145°46′E, on *Ceriops tagal*, 1976, *D. Tarte* (BRIU2252NS); North Mission Beach, 17°52′S, 146°06′E, on *Rhizophora* sp., 1979, *NCS* (BRIU2663NS); Hinchinbrook I, 18°14′S, 146°13′E, on *Lumnitzera* sp., 1979, *GNS* (BRIU3465NS); Townsville, 19°15′S, 146°50′E, on *Rhizophora stylosa*, 1975, *B. Ballment* (BRIU3117NS); Bowen, Dry Ck Rd, 20°04′S, 148°22′E, on *Rhizophora apiculata*, 1979, *GNS* (BRIU3133NS); Eimeo, Sunset Beach, 21°09′S, 149°09′E, on *Rhizophora* sp., 1976, *GNS* (BRIU1353NS); Keppel Sands, 23°21′S, 150°47′E, on *Avicennia marina*, 1975, *RWR* (BRIU900RR); Port Alma, 23°35′S, 150°51′E, on *Rhizophora* sp., 1975, *RWR* (BRIU695RR); Gladstone, 23°50′S, 151°16′E, on *Rhizophora stylosa*, 1980, *GNS* (BRIU3456NS); Turkey, 24°06′S, 151°37′E, on *Ceriops tagal*, 1975, *GNS* (BRIU1271); Round Hill Head, 24°10′S, 151°54′E, on *Rhizophora stylosa*, 1975, *RWR* (BRIU916RR); Burnett Hds, 24°45′S, 152°25′E, on *Casuarina* sp., 1975, *GNS* (BRIU4296); Burrum Hds, 25°10′S, 152°35′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1121NS); Urangan, 25°19′S, 152°55′E, on *Callitris columellaris*, 1978, *GNS* (BRIU2840NS); Kin Kin Ck, 26°13′S, 153°00′E, on *Avicennia marina*, 1979, *GNS* (BRIU3214NS); Maroochy R, 26°42′S, 153°05′E, on *Avicennia marina*, 1976, *GNS* (BRIU1335NS); Bribie I, 27°02′S, 153°08′E, on *Lumnitzera racemosa*, 1978, *GNS* (BRIU2283NS); Whyte I, 27°23′S, 153°10′E, on *Avicennia marina*, 1978, *GNS* (BRIU2594NS); Mud I, 27°20′S, 153°15′E, on *Avicennia marina*, 1978, *GNS* (BRIU2760NS); Coochiemudlo I, 27°32′S, 153°17′E, on *Callitris columellaris*, 1975, *GNS* (????????); Bilinga, 28°08′S, 153°31′E, on dead tree, 1981, *AA* (BRIU4276NS); Norries Hd, 28°18′S, 153°34′E, on metamorphic rock, 1980, *GNS* (BRIU3665NS); Byron Bay, 28°39′S, 153°37′E, on dune shrub, 1978, *RWR* (BRIU3883*NS); Yamba, 29°27′S, 153°20′E, on *Avicennia marina*, 1977, *GNS* (BRIU3177NS); Port Macquarie, 31°27′S, 152°54′E, on *Ficus* sp., 1975, *JAE* (JAE 1089); Hunter R., Ash I, 32°56′S, 151°46′E, 1845, *J. P. Verreaux* (PC).

var. ***leiodea*** (Nyl.) N. Stevens, **comb. nov.** Plate 11, fig. 6; Plate 12, fig. 8; Plate 15, fig. 3.

Ramalina subfraxinea [subsp.] *leiodea* Nyl. in *Bull. Soc. linn. Normandie* II, **4**: 141 (1870). – *Ramalina leiodea* (Nyl.) Nyl., *Lich. Nov. Zel.*: 22 (1888). Type: New Caledonia, 'Donné par le Musée Colonial', 1861, *Deplanche* s.n. (PC! – lectotype; boninic acid aggregate).

Ramalina boninensis Asah. in *J. Jap. Bot.* **14**: 253 (1938). Type: Bonin Islands, Ogasawara I., Hahajima, 1936, *Kusaka* s.n. (TNS! – holotype; boninic acid aggregate).

Ramalina boninensis f. *subcalicariformis* Asah. in *J. Jap. Bot.* **15**: 211 (1939). Type: Bonin Islands, Ogasawara I., Hahajima, 1936, *Kusaka* s.n. (TNS! – holotype).

Thallus corticolous, grey-green, caespitose, rigid, erect to subpendulous, up to 4 cm high, exceptionally to 9 cm; branching subdichotomous, sparse to moderate; branch width (0·5–)2–4 mm, branches compressed, flat or canaliculate when narrow, apices attenuate; surface matt, smooth to rugose, short linear pseudocyphellae sometimes present; holdfast delimited; soralia absent.

Apothecia common, marginal and subterminal, rarely laminal, small thalli produce subterminal apothecia subtended by a spur; disc 2–3 mm diam., concave to plane; margin entire or incised at maturity; spores ellipsoid, straight or slightly curved; 10–12(–16) × 4–5 μm.

Chemistry. Boninic acid (M), 2-0-methylsekikaic acid (m), 2,4'-di-0-methylnorsekikaic acid (m), 4'-0-methylpaludosic acid (m), 4,4'-di-0-methylcryptochlorophaeic acid (m), and usnic acid.

Remarks. Prior to the present study *R. subfraxinea* var. *leiodea* had species status. The history of this taxon, however, is one of name changing since its first identification by Nylander in 1859. Specimens of this taxon have been identified as follows: *Ramalina Ecklonii* Sprengel (Nylander, 1859); *Ramalina calicaris* f. *Ecklonii* (Sprengel) Nyl. (Nylander, 1861); *Ramalina subfraxinea* [subsp.] *leiodea* Nyl. (Nylander, 1870) and *Ramalina leiodea* Nyl. (Nylander, 1888).

A thorough investigation of specimens of this taxon held at PC and H was undertaken by Stevens (1982). It was found that two acid races (viz. boninic acid and cryptochlorophaeic acid) were present in taxa bearing this name. Because the material designated lectotype contained boninic acid, the species *R. boninensis* Asah. and *R. boninensis* f. *subcalicariformis* were reduced to synonomy at that time.

Krog & Swinscow (1976) commented on the similarity between the East African taxon *R. maritima* and material from Bourbon I. and Mauritius. Specimens from the latter two areas had been identified as *R. subfraxinea* by Nylander (1870). Chemical analysis showed they contained boninic acid (Krog & Swinscow, 1976), which was also confirmed in this study (see comments under *R. subfraxinea* var. *subfraxinea*). Morphologically and chemically *R. subfraxinea* var. *leiodea* and *R. maritima* resemble one another but differences in spore size sets them apart, the former taxon produces spores in the range 8–16 × 4–5 μm, whereas *R. maritima* spores lie in the range 18–25 × 5–6 μm.

Distribution and habitat. Ramalina subfraxinea var. *leiodea* occurs from latitudes 18°S–29°S along the eastern coastline of Australia (Fig. 28), with its most frequent occurrence in the subtropics. The distribution range overlaps that of *R. subfraxinea* var. *confirmata*, a mainly tropical taxon which extends into the subtropics so that both taxa are sympatric for a large part of their distribution (Fig. 31).

This taxon occurs on mangroves (*Avicennia marina* and *Rhizophora stylosa*) and on coastal trees (*Callitris columellaris* and *Casuarina equisetifolia*).

World distribution. Bonin Is, Marianas Is, Mauritius, Réunion I., Australia, Lord Howe I., Norfolk I., New Caledonia, New Hebrides, Cook Is (Rarotonga), and Hawaii.

Queensland: Hinchinbrook I, 18°14′S, 146°50′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3479NS); Long I, Whitsunday Group, 20°21′S, 148°51′E, on coastal shrub, 1979, *A. B. Cribb* (BRIU3225NS); Eimeo, 21°09′S, 149°09′E, on *Ceriops tagal*, 1977, *GNS* (BRIU3155NS); St Lawrence, 22°20′S, 149°32′E, on *Ceriops tagal*, 1976, *GNS* (BRIU2455NS); Gladstone, 23°51′S, 151°16′E, on *Rhizophora stylosa*, 1980, *GNS* (BRIU3285NS); Turkey, 24°06′S, 151°38′E, on *Rhizophora stylosa*, 1975, *GNS* (BRIU1148NS); Burnett Hds, 24°46′S, 152°25′E, on *Rhizophora stylosa*, 1976, *GNS* (BRIU4296NS); Toogoom, 25°15′S, 152°40′E, on *Callitris columellaris*, 1983, *GNS* (BRIU4152NS); Urangan, 25°19′S, 152°55′E, on *Callitris columellaris*, 1978, *GNS* (BRIU2884NS); Kin Kin Ck, 26°13′S, 153° on *Casuarina* sp., 1979, *GNS* (BRIU3223NS); Noosa Hds, 26°23′S, 153°05′E, on rain-forest tree, 1980, *GNS* (BRIU3547NS); Moreton I, 27°20′S, 153°25′E, on *Callitris columellaris*, 1980, *RWR* (BRIU3476NS); Cape Byron, 28°37′S, 153°36′E, on *Acacia* sp., 1980, *RWR* (BRIU3883NS). **New South Wales**: Yamba, 29°27′S, 153°20′E, on *Avicennia marina*, 1977, *GNS* (BRIU2122NS); Broomes Hd, 29°37′S, 153°20′E, on *Casuarina* sp., 1982, *GNS* (BRIU4311NS).

var. ***norstictica*** N. Stevens, **var. nov.** Plate 11, fig. 8.

Thallus corticolus, viridi-griseus caespitosus rigidus erectus vel subpedulus, 1·5–6·5 cm longus, ramificatione subdichotoma sparsa vel mediocri; rami lati ad 1–1·5 mm, applanati vel canaliculati, apice attenuati; superficies impolita, laevigata vel rugosa et crassa, pseudocyphellis laminalibus linearibus, ad fundamenta, tubercularis pseudocyphellis marginalibus, sparsa vel numerosa; soralia nulla. Apothecia numerosa, marginalia vel subterminalia, calcarata; discus ad 3–5 mm in diametro, concava vel plana vel convexa; sporae ellipsoideae vel raro fusiformae, rectae vel raro curvatae, 9–16(–20) × 3·5–5·5 μm. Acidum norsticticum ± connorsticticum et usnicum continens.

Holotype: Australia, Queensland, St Lawrence, on *Ceriops tagal*, 11 July 1978, *G. N. Stevens* 2459 (MEL 1048088!).

Thallus corticolous, pale green to green-grey, caespitose, rigid erect to subpendulous, 1·5–6·5 cm long; branching subdichotomous, sparse to moderate; branch width 1–1·5 mm, compressed, flat or canaliculate, some marginal splitting of the branches between the upper and lower surfaces, apices attenuate; surface matt, smooth to rugose and coarse, with or without basal pseudocyphellae, tuberculate pseudocyphellae marginal few to many when present; holdfast delimited; soralia absent.

Apothecia common, marginal and subterminal, some spurred; disc 3–5 mm diam., concave, plane to convex; margin thin, with or without lateral branchlets; spores ellipsoid rarely fusiform, straight, rarely curved, 9–16(–20) × 3·5–5·5 μm.

Chemistry. Norstictic acid, ± connorstictic acid, and usnic acid.

Remarks. This taxon is an Australian endemic; examination of esorediate maritime taxa from overseas herbaria failed to find any norstictic acid taxon which resembled it. In Australia the taxon closest to it morphologically is *R. subfraxinea* var. *subfraxinea*. Both taxa are sympatric for part of their distribution and have similar habitats so that the similarity in morphology could be due to convergent morphology under the same environmental pressures (Fig. 31).

Ramalina subfraxinea var. *norstictica* produces branchlets around the margins of the apothecia at times, but this is not a constant character and cannot be used taxonomically. Splitting along the margins of the branches also occurs, but this is also common in the salazinic acid taxon belonging to the *R. subfraxinea* complex. The rank of variety was given to this norstictic acid taxon because of its distinct chemistry and its geographical occurrence along the northern Australian coastline (Figs 29, 31).

Distribution and habitat. Ramalina subfraxinea var. *norstictica* occurs along the northern and

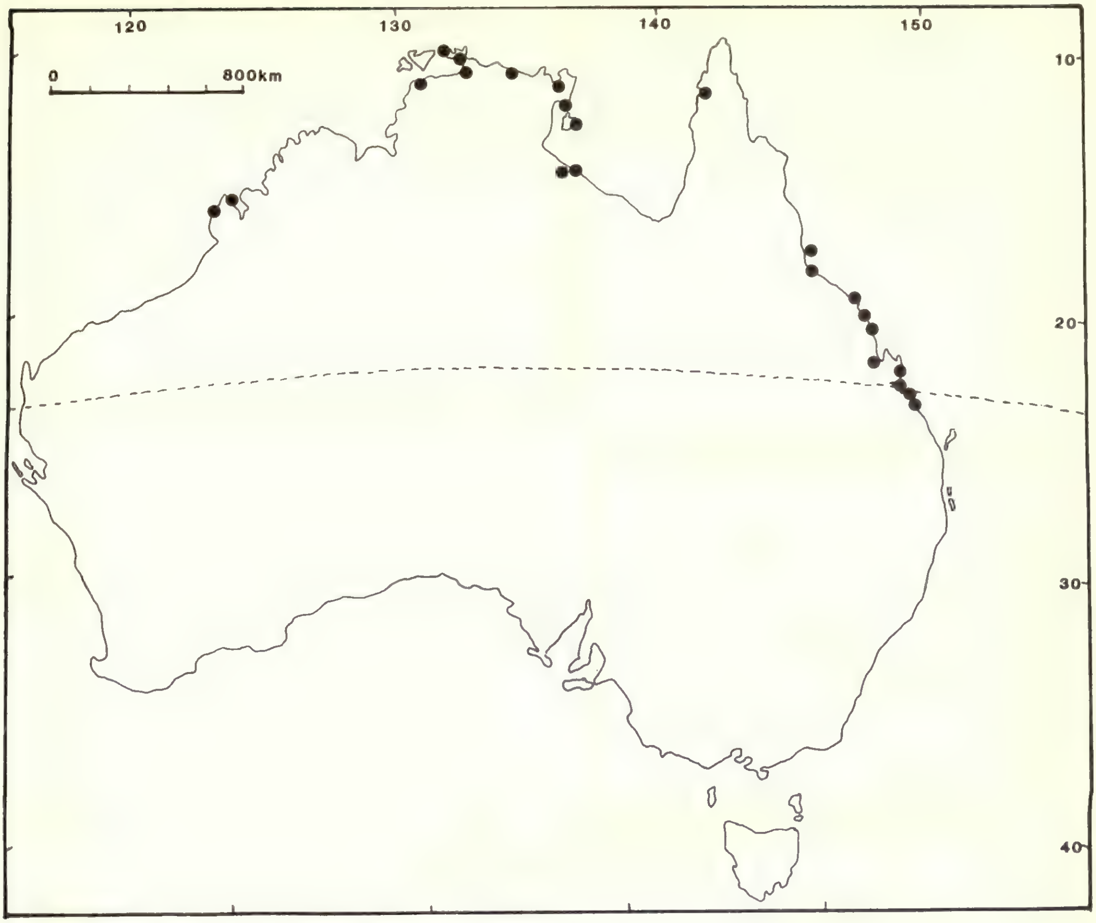


Fig. 29 Distribution of *R. subfraxinea* var. *norstictica*.

eastern coastlines of Australia (Fig. 29). Its absence from an area between latitudes 17°–11°S on the eastern coast is an anomaly since it is found on the northern coastline between these latitudes. It is in fact replaced by the salazinic acid taxon *R. tropica* in this section of the eastern coastline. It could be inferred that a change from one depsidone to the other came about with change in environmental pressures as norstictic acid is almost certainly a biogenetic precursor of salazinic acid (Elix, in litt.). However, no thalli were found containing both norstictic acid and salazinic acid.

The morphology of the norstictic acid taxon is variable and appears to be ecophenotypic, ranging from thalli with narrow, canaliculate branches bearing subterminal apothecia, to broad, flat, branched thalli bearing large, marginal apothecia. Tuberculate pseudocyphellae occur on thalli growing in very dry or polluted areas. The spores of *R. subfraxinea* var. *norstictica* are intermediate (in both size and shape) between the small ellipsoid spores of *R. subfraxinea* var. *confirmata* and the large fusiform spores of *R. tropica*.

World distribution. Australia.

Western Australia: Cygnet Bay, 16°35′S, 123°02′E, on *Bruguiera* sp., 1980, *S. Kenneally* (PER001045); Swan Point, 16°25′S, 123°02′E, 1906, *W. V. Fitzgerald* (NSW L4117). **Northern Territory**: Port Darwin, 12°26′S, 130°48′E, 1890, *M. Holtze* (MEL 9477); East Alligator R. 12°08′S, 132°40′E, on *Ceriops tagal*, 1979, *E. Hegerl*, (BRIU3114NS); Cobourg Pen., Caiman Ck, 11°25′S, 132°06′E, on mangrove, 1968, *J. R. Maconochie* (MEL100288); Tomkinson R, 12°13′S, 134°16′E, on *Avicennia* sp., 1975, *D. Grace* (MEL1012777); Melville Bay, 12°15′S, 136°40′E, on *Ceriops tagal*, 1948, *R. L. Specht* (SA 97528120);

Groote Eylandt, Hemple Bay, 13°49′S, 136°38′E, on mangroves, 1948, *R. L. Specht* (SA 97527533); Carrington Ck, 15°44′S, 136°36′E, on mangroves, *McKay* (MEL102350). **Queensland**: Weipa, 12°38′S, 141°55′E, on mangroves, 1974, *R. L. Specht* (BRIU3584NS); Hinchinbrook I, 18°22′S, 146°15′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3185NS); Townsville, 19°15′S, 146°50′E, on *Ceriops tagal,* 1975, *B. Ballment* (BRIU3120NS); Bowen, Dry Ck Rd, 20°04′S, 148°22′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3141NS); Mackay, Eimeo, 21°09′S, 149°09′E, on *Ceriops tagal*, 1976, *GNS* (BRIU3434NS); St Lawrence, 22°21′S, 149°32′E, on *Excoecaria agallocha*, 1976, *GNS* (BRIU2463NS); Corio Bay, 22°58′S, 150°46′E, on *Rhizophora* sp., 1975, *D. Tarte* (BRIU1170NS); Keppel Sands, 23°21′S, 150°47′E, on *Excoecaria agallocha*, 1975, *RWR* (BRIU760RR); Port Alma, 23°35′S, 150°51′E, on *Ceriops tagal,* 1975, *RWR* (BRIU1039RR); Gladstone, 23°50′S, 151°16′E, on *Rhizophora stylosa*, 1980, *GNS* (BRIU3259NS).

20. *Ramalina tropica* N. Stevens, sp. nov. Plate 12, figs 1, 2, 6.

Thallus corticolus et saxicolus, virentes-pallido caespitosus rigidus erectus, usque ad 4·0 cm altus, ramificatione subdichotoma sparsa vel mediocri; rami lati ad 0·5–1·0 mm, subteretes vel teretes vel raro planares, apice attenuati curvi; superficies impolita vel nitida, laevigata vel rugosa, pseudocyphellis laminalibus linearibus instructa aut sine pseudocyphellis; soralia nulla. Apothecia raro aut vulgariter, subterminalia et calcarata vel marginala, ramis flexuosis insidentes; discus ad (1–)1·5–3·0 mm in diametro, planus vel convexus; sporae fusiformae, rectae, 11–18(–22) × 3·8–5(–6) μm. Acidum salazinicum ± protocetraricum et usnicum continens.

Holotype: Australia, Queensland, Lizard Island, 26 December 1974, *R. L. Specht* (MEL 1048087!).

Thallus corticolous, or saxicolous, pale green, caespitose, rigid, erect, usually to 2 cm high, exceptionally to 4 cm; branching subdichotomous, sparse to moderate, branches arising from the base with lateral branchlets common; branch width 0·5–1·0 mm, subterete to almost terete, rarely flat, never canaliculate, some marginal splitting of the branches between the upper and lower surfaces, apices tapering distally, often recurved; surface matt or shiny, smooth to rugose, fine linear pseudocyphellae and tuberculate pseudocyphellae sometimes present; holdfast delimited; soralia absent.

Apothecia rare to common, marginal on flexuous branches or subterminal with the branch continuing to grow forming a long curved spur up to 10 mm, disc (1–)1·5–3·0 mm diam., plane to convex, some assuming a helmet shape; margin entire; spores fusiform, rarely ellipsoid, straight, rarely bent, some appearing as 3-celled; 12–18(–22) × 3·8–5(–6) μm.

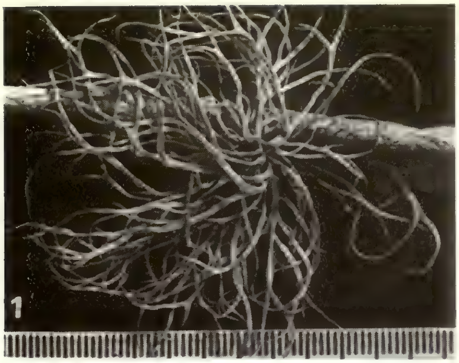
Chemistry. Salazinic acid, ± protocetraric acid, and usnic acid.

Remarks. The erection of this new species has been made cautiously. There were several reasons for making this decision rather than regarding the salazinic acid taxon as another chemical variety of the *R. subfraxinea* complex. (i) Morphologically the four depside taxa and the norstictic acid taxon closely resemble one another in producing thalli with flat or canaliculate branches, whereas the salazinic acid taxon mainly produces subterete branches and in some saxicolous forms, terete branches; (ii) The large size of the spores is in excess of the size produced by any of the other taxa in the complex; (iii) the distinct depsidone chemistry.

Ramalina tropica resembles the East African species *R. fecunda* Krog & Swinscow, which contains salazinic acid and produces large fusiform spores. However, the latter taxon has branches which are flat or canaliculate, not subterete (Krog, in litt).

Other maritime species producing salazinic acid are *R. zollingeri* Szat. (Java), *R. sideriza* Magnusson (Hawaii), and undescribed material (Fiji). Before any affinities could be established between these taxa and *R. tropica* more material would need to be examined.

Plate 12 Thallus growth forms in the Australian Ramalinae. Scale in mm. Fig. 1 *R. tropica* (sterile form). Fig. 2 *R. tropica* (type specimen). Fig. 3 *R. subfraxinea* var. *subfraxinea* (top – narrow form; bottom – broad form). Fig. 4 *R. subfraxinea* var. *confirmata* (broad form). Fig. 5 *R. subfraxinea* var. *norstictica* (sparse apothecia). Fig. 6 *R. tropica* (terete, inland form). Fig. 7 *R. subfraxinea* var. *subfraxinea* (broad form). Fig. 8 *R. subfraxinea* var. *leiodea*. Fig. 9 *R. subfraxinea* var. *norstictica*. Fig. 10 *R. subfraxinea* var. *confirmata*.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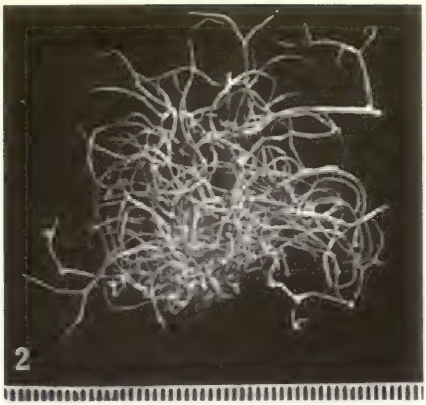
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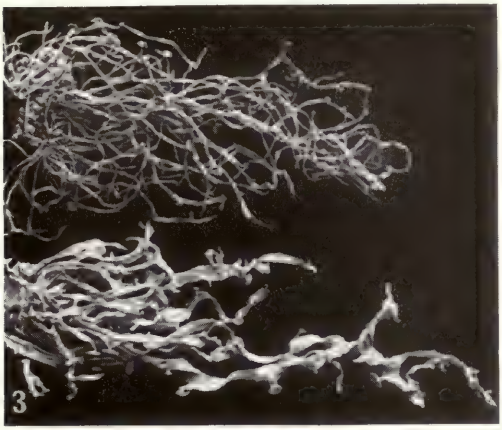
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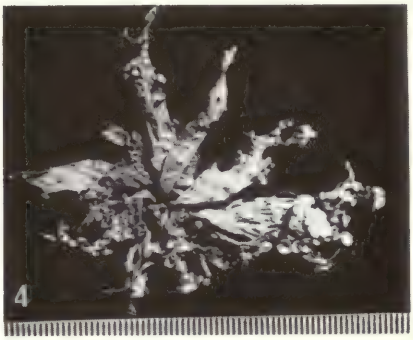
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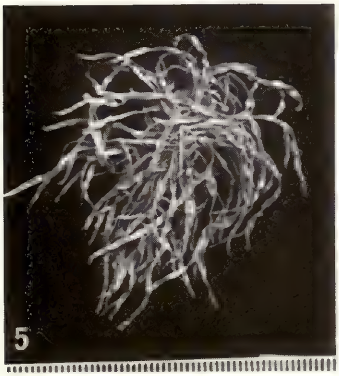
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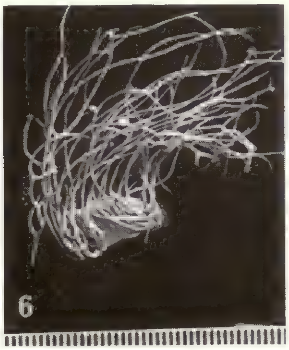
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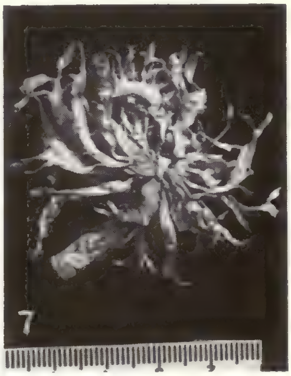
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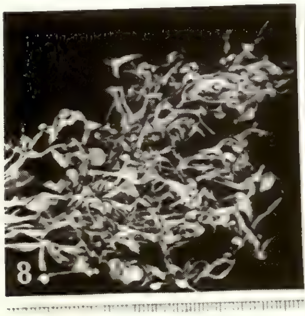
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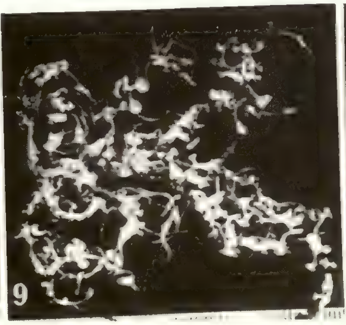
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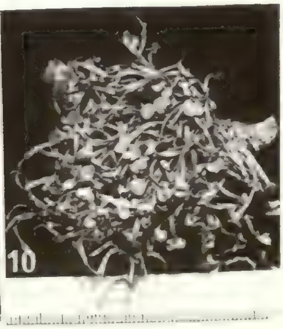
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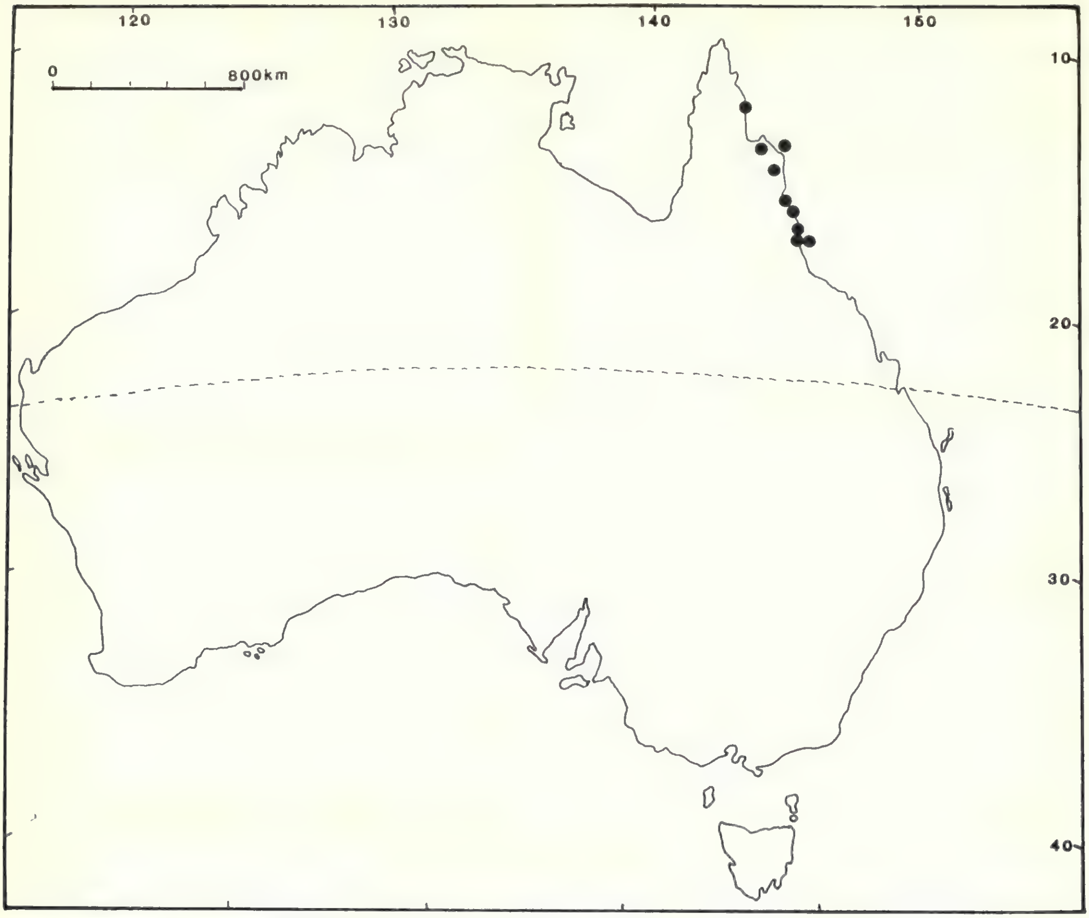


Fig. 30 Distribution of *R. tropica*.

Distribution and habitat. The distribution of *R. tropica* is restricted to an area on the eastern coastline of Cape York between latitudes 13°S (Claudie River) and 18°S (Hinchinbrook I.) [Figs 30, 31]. Because of its restricted distribution range compared with that of the other *R. subfraxinea* taxa, indications are that *R. tropica* may have certain habitat requirements not found elsewhere along the coast.

Ramalina tropica is both corticolous and saxicolous over its range, occurring both coastally and on the coastal hills. Morphologically variable, it produces several morphotypes, e.g. at latitude 18°S it is sympatric with the rest of the *R. subfraxinea* complex and closely resembles these taxa, illustrating the phenomenon of convergent morphology. At latitude 16°S it is sympatric with *R. subfraxinea* var. *subfraxinea* and both produce a straggly, wiry growth form with dense lateral branchlets; however, the characteristic rounding of the branches in *R. tropica* is detectable when comparing the thalli with flattened branches of *R. subfraxinea* var. *subfraxinea* thalli.

Corticolous thalli of *R. tropica* attain their maximum length of 4·0 cm on Lizard Island in the mangrove environment where *Ceriops tagal* is the usual phorophyte. The branches are very narrow, subterete, and bear marginal apothecia subtended by markedly attenuate recurved branch apices (Plate 12, fig. 1). *Ramalina tropica* also grows on granite rock on Lizard Island, but the saxicolous morph differs from the corticolous morph in producing a rigid, sparsely branched thallus, bearing few or no apothecia.

Inland collections of this taxon were made at Abbey Peak (650 m altitude) at latitude 14°18′S,

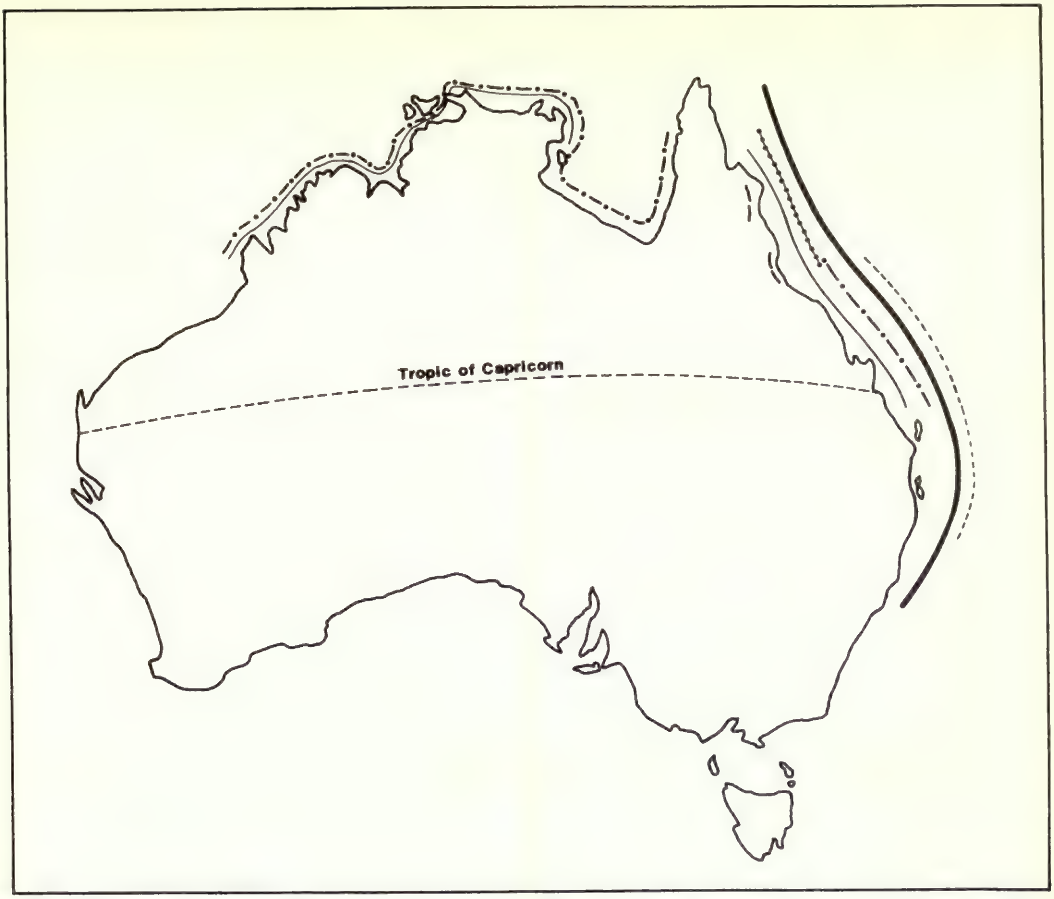
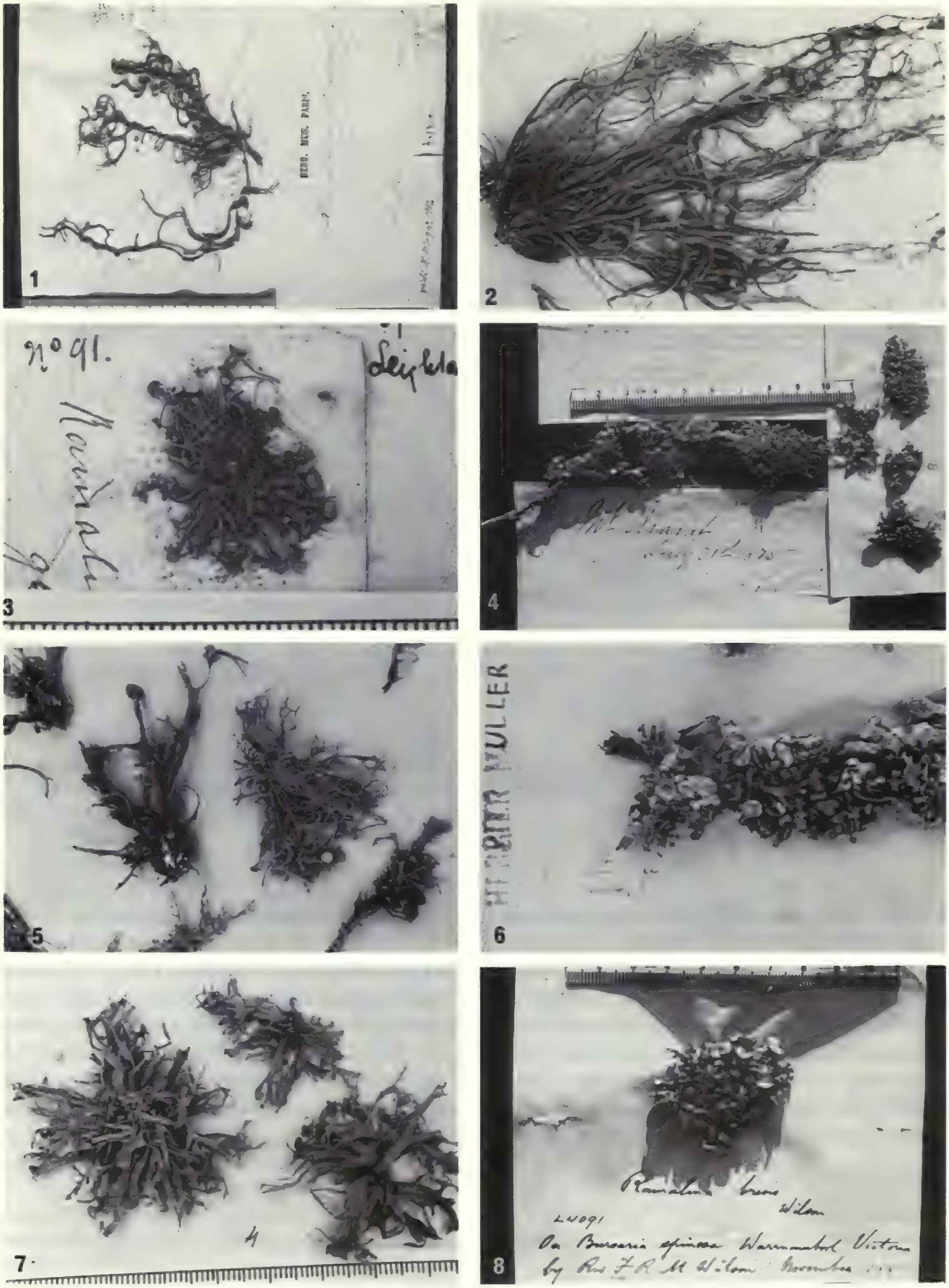


Fig. 31 Distribution ranges of the six acid taxa in the *R. subfraxinea* complex: var. *subfraxinea* (sekikaic acid race) ——; var. *subfraxinea* (divaricatic acid race) ——; var. *norstictica* ·—·—·—·; *var. confirmata* ——; var. *leiodea* ----; *R. tropica* —·—·.

where it occurs on windblown shrubs at the summit, and at Lighthouse Mountain (400 m altitude) at latitude 16°38′S where it occurs on granite rock at the summit. These morphotypes are more terete than coastal thalli and produce a thicker cortex. Increased thickness of the cortex is a feature reported by Rundel (1982) as an adaptation to decrease the rate of evaporation from the thallus in extreme conditions where selection for low rates of evaporative loss is more important than rapid rate of water uptake. The terete branches and fasciculate growth form (Plate 12, fig. 6) may be a response to increased moisture stress as discussed by Sheard (1978); these adaptations would ensure that less thallus area was effected by heat in an environment which is exposed to extreme heat and dryness for long periods.

World distribution. Australia.

Queensland: Claudie River, Charlie Taylors Landing, 12°36′S, 143°42′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4111NS); Abbey Peak, 14°18′S, 144°30′E, on shrub on summit, 1983, *C. McCracken* (BRIU4239NS); Lizard I, 14°41′S, 145°28′E, on granite, 1974, *R. L. Specht* (BRIU3780NS); Lizard I, 14°41′S, 145°28′E, on mangroves, 1974, *R. L. Specht* (MEL1048087) Type; Lighthouse Mt, between Mt Carbine & Mt Molloy, 16°35′S, 145°13′E, on granite, 1983, *C. McCracken* (BRIU4218NS); Daintree R. south branch, 16°18′S, 145°24′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4189NS); Mossman Rifle Range, 16°29′S, 145°25′E, on *Ceriops tagal*, 1983, *GNS* (BRIU4188NS); South Mission Beach, 17°56′S, 146°05′E, on rain-forest tree, 1983, *GNS* (BRIU4163NS); Murray R. 18°02′S, 146°03′E, on *Ceriops tagal*, 1979, *D. Tarte* (BRIU3159NS); Hinchinbrook I, 18°20′S, 146°15′E, on *Ceriops tagal*, 1979, *GNS* (BRIU3160NS).


1
2
No 91.
3
4
HERBIER MULLER
5
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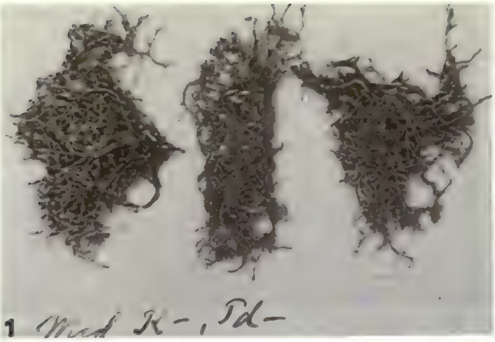
7
8
Ramalina brevis Wilson

Plate 13 Photographs of Australian *Ramalina* types. Scale in mm. Fig. 1 *R. australiensis* (PC). Fig. 2 *R. myrioclada* (G). Fig. 3 *R. exiguella* (BRI). Fig. 4 *R. glaucescens* (M). Fig. 5 *R. lacerata* (G). Fig. 6 *R. leiodea* var. *fastigiatula* (G). Fig. 7 *R. calicaris* var. *australica* (H). Fig. 8 *R. brevis* (NSW).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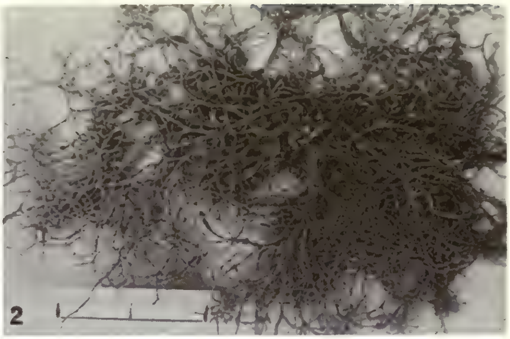
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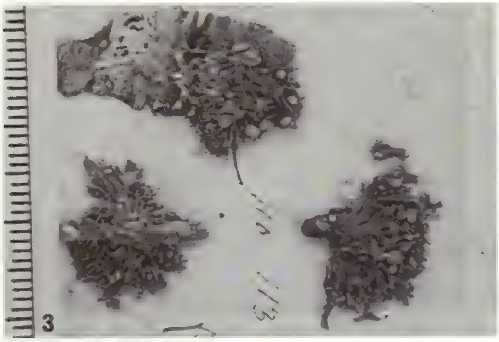
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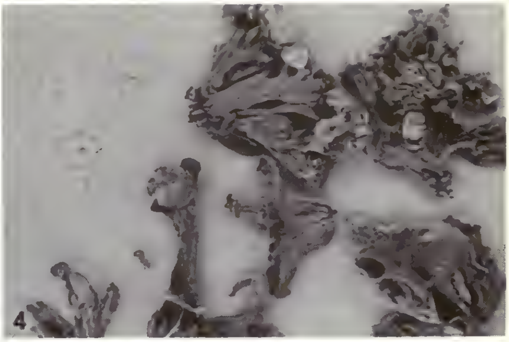
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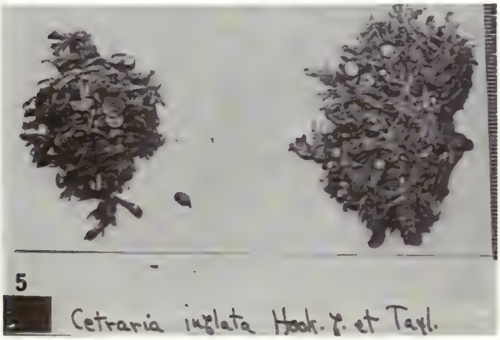
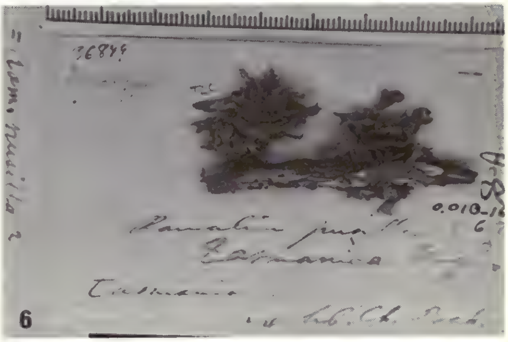

5
Cetraria inflata Hook. f. et Tayl.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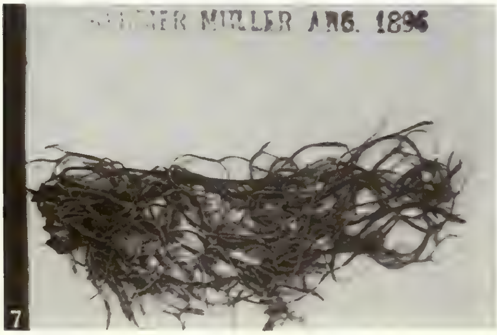
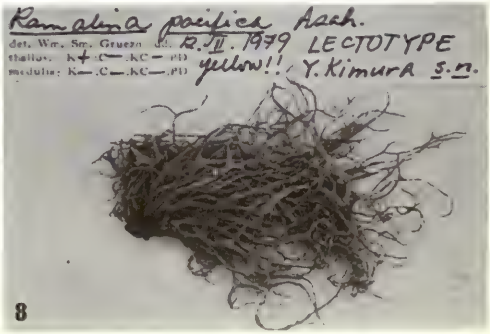
Tasmania
0.010-1


7
MILLER ANG. 1896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Ramalina pacifica Asch.
det. Wm. Sm. Gruezo d. R.II.1979
LECTOTYPE
thallus: K+ C— KC— PD
medulla: K— C— KC— PD
yellow!!
Y. Kimura s.n.

Plate 14 Photographs of Australian *Ramalina* types. Scale in mm. Fig. 1 *R. farinacea* var. *squarrosa* (G). Fig. 2 *R. farinacea* var. *dendroides* (G). Fig. 3 *R. perpusilla* (BRI). Fig. 4 *R. fissa* (G). Fig. 5 *R. inflata* (FH). Fig. 6 *R. tasmanica* (H). Fig. 7 *R. nervulosa* var. *nervulosa* (G). Fig. 8 *R. pacifica* (TNS).

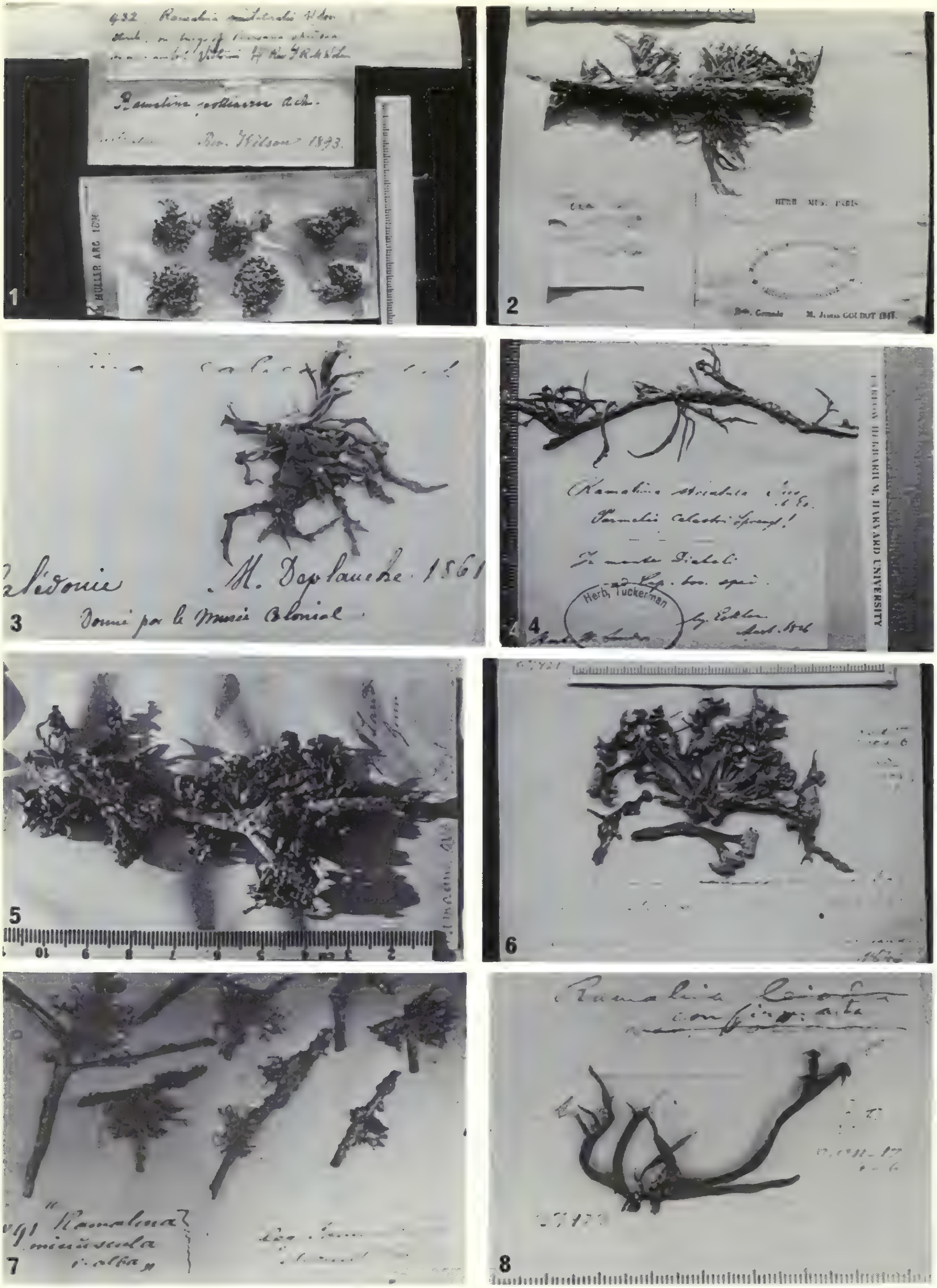
1
MULLER ARG
Rev. Wilson 1893.
2
HERB. MUS. PARIS
3
M. Deplanche 1861
Donné par le Musée Colonial
4
Herb. Tuckerman
FARLOW HERBARIUM, HARVARD UNIVERSITY
5
6
7
Ramalina minuscula v. alba
8
Ramalina
confirmata

Plate 15 Photographs of Australian *Ramalina* types. Scale in mm. Fig. 1 *R. unilateralis* (G). Fig. 2 *R. subfraxinea* (PC). Fig. 3 *R. leiodea* (PC). Fig. 4 *R. celastri* (FH – isotype). Fig. 5 *R. ovalis* (BM). Fig. 6 *R. fraxinea****R. confirmata* (H – isotype). Fig. 7 *R. minscula* var. *alba* (WELT). Fig. 8 *R. fraxinea****R. confirmata* (H – lectotype).

Appendix. Disposition of excluded *Ramalina* taxa

The position of other *Ramalina* taxa recorded from Australia in Wetmore (1963), and Weber & Wetmore (1972) is indicated below.

R. anceps = *R. australiensis* Nyl. or *R. filicaulis* N. Stevens
R. angulosa = *R. australiensis* Nyl.
R. calicaris = *R. glaucescens* Krempelh.
R. calicaris var. *canaliculata* = *R. glaucescens* Krempelh.
R. complanata = *R. subfraxinea* Nyl.
R. confirmata = *R. subfraxinea* var. *confirmata* (Nyl.) N. Stevens.
R. dendriscoides = *R. tenella* Müll. Arg. or *R. peruviana* Ach.
R. dendriscoides var. *minor* = *R. tenella* Müll. Arg. or *R. peruviana* Ach.
R. dilacerata var. *alba* = *R. inflata* subsp. *perpusilla* (Stirton) N. Stevens
R. ecklonii = *R. celastri* (Sprengel) Krog & Swinscow
R. ecklonii var. *membranacea* = *R. celastri* (Sprengel) Krog & Swinscow
R. ecklonii var. *ovalis* = *R. celastri* subsp. *ovalis* (J. D. Hook & Taylor) N. Stevens
R. ecklonii var. *tenuissima* = *R. celastri* (Sprengel) Krog & Swinscow
R. fastigiata = *R. glaucescens* Krempelh.
R. fraxinea = *R. glaucescens* Krempelh.
R. fraxinea var. *ampliata* = *R. glaucescens* Krempelh.
R. fraxinea f. *platyna* = *R. fissa* (Müll. Arg.) Vainio
R. fraxinea var. *taeniata* = *R. glaucescens* Krempelh.
R. furcellata = *R. australiensis* Nyl.
R. geniculata = *R. inflata* J. D. Hook. & Taylor
R. geniculata var. *olivacea* = *R. inflata* subsp. *perpusilla* (Stirton) N. Stevens
R. gracilenta = *R. exiguella* Stirton
R. gracilis = *R. exiguella* Stirton or *R. filicaulis* N. Stevens
R. homalea = unknown?
R. inflata var. *gracilis* = *R. inflata* (J. D. Hook. & Taylor) J. D. Hook. & Taylor
R. intermedia = *R. inflata* subsp. *australis* N. Stevens
R. javanica = *R. peruviana* Ach.
R. linearis = *R. celastri* (Sprengel) Krog & Swinscow
R. pollinaria = *R. unilateralis* F. Wilson
R. polymorpha = unknown
R. polymorpha f. *emplecta* = unknown
R. pusilla = *R. inflata* subsp. *australis* N. Stevens
R. scopulorum = *R. subfraxinea* Nyl. var. ?
R. scopulorum var. *cuspidata* = *R. subfraxinea* Nyl. var. ?
R. scopulorum var. *subfarinacea* = *R. pacifica* Asah.
R. tayloriana = *R. nervulosa* var. *luciae* (Molho et al.) N. Stevens
R. usnea = *R. australiensis* Nyl.
R. usneoides = *R. australiensis* Nyl.
R. yemensis = *R. celastri* (Sprengel) Krog & Swinscow
R. yemensis var. *ovalis* = *R. celastri* subsp. *ovalis* (J. D. Hook. & Taylor) N. Stevens

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(Macquarie Island Ramalinae), R. Specht, J. Berjak (South African Ramalinae), G. Kantvilas (Tasmanian Ramalinae) and A. Archer, E. Dahl, J. Elix, R. Rogers, N. Sammy, C. Scarlett, H. Streimann (mainland Australia Ramalinae). I am grateful to Dr A. Henssen for supplying two of the photographs used in this paper. All SEM and TEM photographs were taken by Mr J. Hardy of the Electron Microscope Centre, University of Queensland. I thank M. Lamy for supplying information from the Verreaux journals.

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An annotated list of vascular plants collected in the valleys south of Mt Everest

Georg Miehe

Department of Geography, University of Göttingen, Goldschmidtstrasse 5, D-3400
Göttingen, West Germany

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Synopsis

An alphabetical checklist has been compiled, based mainly on collections in the British Museum (Natural History), of plants at altitudes above 2300 m in east central Nepal, in the upper catchment of the Dudh Kosi and the transverse valleys to the south of Mt Everest, eastwards to 87° 10′E. At least 1020 species of phanerogams have been collected in this area. Information is provided on life forms and associated plant formations, and voucher specimens are cited to validate the records. Introductory notes are provided on the altitudinal zonation of the vegetation and on the tree-line. The cloud forests on the humid southern side of the main Himalayan range have a potential (natural) climatic tree-line which is at *c.* 4400 m on sunny slopes and 200 m lower on shady slopes, as is typical for humid mountains north of the tropics. The upper catchment of the Dudh Kosi, which is known as the Khumbu Himal, has been deforested on the sunny slopes by the Sherpas, who colonized these valleys from above, by traversing the main range 400 years ago and settling permanently, thereby causing widespread secondary vegetation due to extensive uncontrolled grazing.

Introduction

Delimitation of the area

The valleys south of Mt Everest, Nepal, included in this account of the flora, are shown in Fig. 1. The only ecologically marked delimitation is the northern boundary which is formed by the main Himalayan range. On the northern side there is an arid Tibetan flora, while the south is taken to be a part of the humid east Himalayan flora. The western boundary is the watershed between the Rolwaling valley and the south-west ridge of Mt Numbur, i.e. the ridge to the west of the Lumding Khola. The north-eastern boundary is less definite, nearly coinciding with the eastern extension of the Khumbu Himal map of Erwin Schneider (1965). It includes the alpine belt of the Barun Khola, with all records which were clearly above the upper cloud forest. The altitudinal limit is *c.* 3800 m at about 87° 10′E, south of Chamlang, Amai Dablang, and Kang Taiga; the

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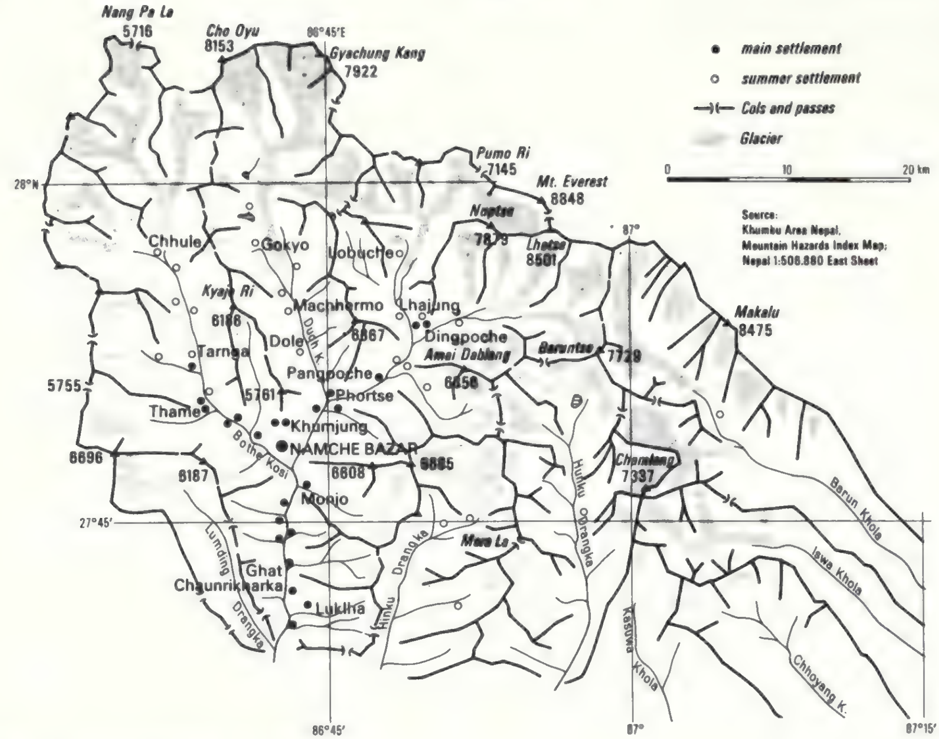

Nang Pa La
5716
Cho Oyu
8153
86°45'E
Gyachung Kang
7922
● main settlement
○ summer settlement
—)(— Cols and passes
Glacier
0
10
20 km
Pumo Ri
7145
Mt. Everest
8848
28°N
Nuptse
7879
Lhotse
8501
87°
Chhule
Gokyo
Lobuche
Kyajo Ri
6186
Machhermo
Lhajung
Dingpoche
Amai Dablang
6856
Dole
Dudh K.
6367
Tarnga
Pangboche
Phortse
5755
5761
Thame
Khumjung
NAMCHE BAZAR
6696
6187
Bothe Kosi
6608
6885
Monjo
27°45'
Lumding
Drangka
Ghat
Chaunrikharka
Luklha
Hinku
Drangka
Mera La
Hunku
Drangka
Baruntse
7720
Makalu
8475
Chamlang
7337
Barun Khola
Iswa Khola
Kasuwa
Khola
Chhoyang K.
86°45'
87°
87°15'

Source:
Khumbu Area Nepal,
Mountain Hazards Index Map;
Nepal 1:506.880 East Sheet

Fig. 1 The valleys south of Mt. Everest.

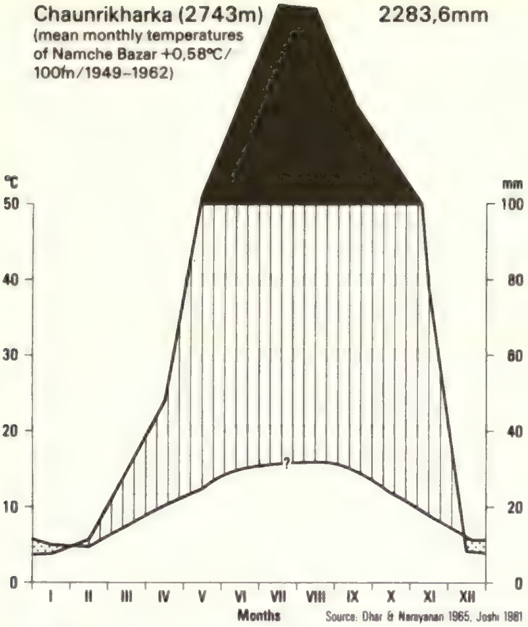
Hinku Drangka (Inugkhu), Hunku Drangka (Hongu), and Iswa Khola run to the south, to join the Arun valley in the east or the Dudh Kosi in the west. Only a few botanists have visited these valleys and their records all belong to the alpine belt and the upper cloud forests.

The vast majority of records are from along the route to Mt Everest. In this area, where the Dudh Kosi valley leads down from the main range between Cho Oyu in the west and Lhotse in the east, the southern limit of the records assembled here is drawn at 2300 m, south of Chaunrikharka. The Dudh Kosi gorge south of Namche Bazar is known as Pharak, while the higher catchment of the Dudh Kosi north of 27° 27′N is called Khumbu. The area covered is rather heterogeneous in its floristic pattern. The south-eastern valleys, the Barun Khola and the Iswa Khola, are likely to prove much more humid (like the east Himalayas) than the Khumbu Himal. The latter was classified by Stainton (1972) as belonging to the 'inner valleys', as it shows a degree of rain-shadow effect. The other component contributing to the heterogeneity is man-made, because the valleys of the Khumbu Himal have been cleared to a much greater extent than is typical for the upper cloud forest belt of the southern slope of the main Himalayan range. The more arid and continental aspect may be due in part to the presence of ruderals and weeds, thus reflecting the influence of man.

Outline of the climate

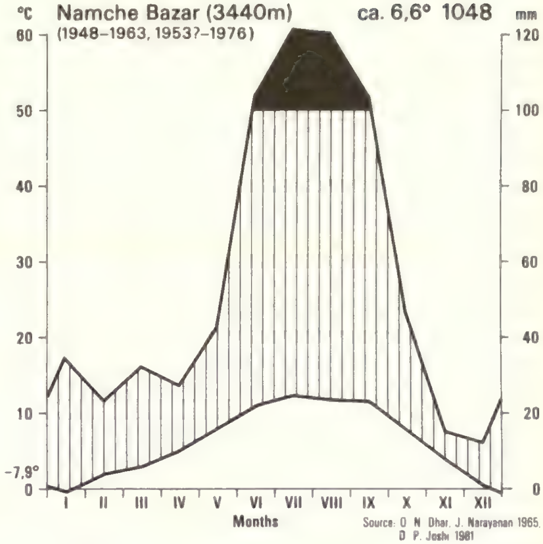
Climatic data in mountain areas are usually inadequate. All meteorological stations are typically situated near settlements, and these are mostly located on valley floors or on less cloudy sites. Thus, for most mountain areas, the data available give the minimum possible rainfall, and are valid only for that small strip on the valley bottom, covering less than 5% of the area.

The data available are summarized in the climatic diagram (Figs 2–4) after Gaussen as drawn by Walter & Lieth (1966), which takes the temperature line as an approach to evapotranspiration. The relation between temperature and rainfall is simplified as 10°C = 20 mm, taken from the mean temperature and the mean monthly rainfall, which is reduced to one-tenth


Chaunrikharka (2743m) 2283,6mm
(mean monthly temperatures of Namche Bazar +0,58°C/100m/1949–1962)

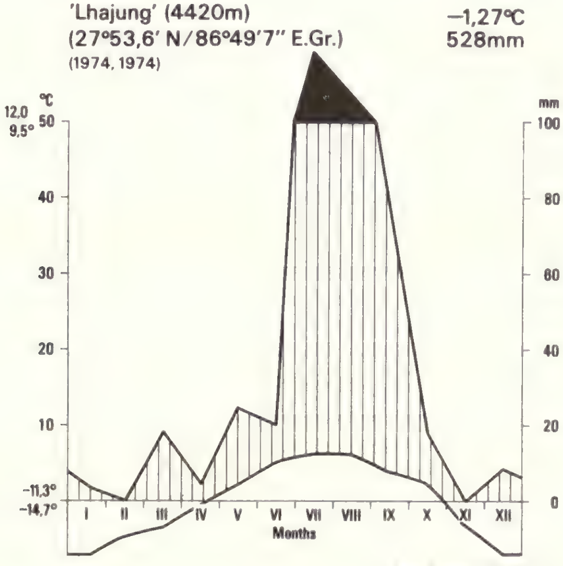
Source: Dhar & Narayanan 1965, Joshi 1981

Fig. 2


Namche Bazar (3440m) ca. 6,6° 1048
(1948–1963, 1953?–1976)

Source: O. N. Dhar, J. Narayanan 1965, D. P. Joshi 1981

Fig. 3


'Lhajung' (4420m) –1,27°C
(27°53,6′ N/86°49′7″ E.Gr.) 528mm
(1974, 1974)

Source: K. Higuchi (Ed.) 1984, App. 3

Fig. 4

Figs 2–4 Climatic diagrams. After Walter & Lieth (1966).

for graphical reasons, if more than 100 mm. Where the temperature line lies above the rainfall line it is relatively arid, whereas in the opposite case it is relatively humid.

From the available data (Dhar & Narayanan, 1965) it is probable that the precipitation decreases from the periphery of the mountain area to the centre, roughly by 50% for every 12 km, but this decrease is also combined with a change in altitude. Thus the decrease is nearly uniform every 1000 m between 2400 and 4400 m. Since the temperature is decreasing also, it does not become drier.

Only in the medium cloud forest belt, at Chaunrikharka is there a dry season in winter, although the precipitation is more than double that at Namche Bazar. At Chaunrikharka 86% of the precipitation is concentrated in the monsoon period, whereas Namche Bazar receives only 74% summer rain. At Namche Bazar, situated in the upper cloud forest belt at 3440 m, relatively dry months may still occur independently of the overall annual rainfall (1961: 921 mm, with no dry month; 1953: 1710 mm, with March and April dry). The number of rainy days per month is higher in Namche Bazar, except in June and July, but fewer millimetres per day fall than in Chaunrikharka. The distribution of heavy precipitation, especially snowfall, is of some economic importance. At Namche Bazar, the months of heavy 24 hour to 72 hour precipitation are those of sowing and harvesting, thus especially before the introduction of the potato (Fürer-Haimendorf, 1964: 8–11), the harvest, which was then of buckwheat and barley, was always uncertain.

Climatic information is also provided by the vegetation, even though we have no exact calibration. Closed plant communities, the presence of epiphytes (especially obligate species that only grow on trees or rocks), and a dense lichen cover can be interpreted as an indicator for humid high-mountain conditions.

Temperature data have rarely been published. For Namche Bazar (3440 m), the mean temperature of the coldest month (January) is −0·4°C, while the mean temperature of the hottest month (July) is 12°C (Joshi, 1982: 400). In the alpine belt at 4420 m, the mean temperature in January is −7·7°C and that of July is nearly 10°C, over a four year period (Higuchi, 1984: appendix).

Valley winds blow every day, setting in mostly between 10 and 11 a.m. and dropping before midnight. They are not as strong as in the transverse gorges like the Karnali or the Kali Gandaki in west and west-central Nepal, but both areas show the same type of clouds, which cover the upper slopes of both sides of the valleys with strips, while the sky over the valley bottoms remains blue.

In monsoon and late monsoon conditions, a closed cloud cover from the south often sweeps into the valleys, nearly as far as closed forests occur, but above 4200 m only strips of cloud on each side of the main valleys advance further up. The valley winds obviously effect the wind-exposed vegetation strongly, as indicated by treeless areas and wind-sculptured trees.

Altitudinal belts of vegetation

The valleys south of Mt Everest are mostly of the same type as those of the European Alps, being typical of high mountains with adequate rainfall to the north of the tropics. Therefore altitudinal limits should be expected to be governed by temperature, decreasing at the rate of 5·8°C per 1000 m and not caused by seasonal drought. This humid type of high mountain is indicated by the interlacing of the belt of glaciers down into the free solifluction belt and down into the alpine belt. The most striking demonstration of that classification is that the free solifluction belt is squeezed into a narrow zone between the glaciers and the vegetation cover of the alpine belt. Thus the upper limit of the characteristic semi-arid altitudinal zone of the high mountains is covered with ice, while the potential lower limit of the solifluction process is suppressed by the closed vegetation cover of forests and alpine scrub (Kuhle, 1978). All belts are interlocked both through natural factors and man's activities. The forest belt is widely cleared and replaced by predominantly alpine associations, and 200 m above the present upper forest line, isolated trees are found growing in alpine scrub.

The alpine belt can be roughly divided into a lower zone of moist alpine scrub (dwarf rhododendrons and prostrate junipers) and an upper zone with *Kobresia pygmaea* mats. Nevertheless, in wind-exposed situations, the Cyperaceae dominated pastures extend down to 3000 m, which is at the maximum about 800 m below the potential upper tree-line, and possibly the result of initial clearance by fires. Dwarf *Rhododendron nivale* cushions are found near the upper limit of the alpine belt at 5500 m. Hence the altitudinal belts are only differentiated by the dominance and not the exclusiveness of their characteristic features.

The lowest altitudinal belt is the forest belt which extends up to roughly 4200 m. It is characterized by epiphytes and should, therefore, be classified as cloud forest. There are both obligate and facultative epiphytes and the latter can be regarded as indicators of a humid climate: creeping ericaceous shrubs are confined to moist soil and are only found on moss-covered tree trunks when this substratum is almost constantly damp through rain and fog. Some of the cloud forest epiphytes even invade the alpine belt, growing in crevices surrounded by cushion-forming alpines, and certain species, mostly found around flushes (*Kobresia schoenoides*, *Rhodiola* spp.), sometimes even become chasmophytic.

Mosses are the dominant epiphytes of the forest belt up to 3000 m. They cover trunks and branches and are colonized by small phanerophytes as facultative epiphytes. Epiphytic ferns and beard lichens occur, but are not dominant. The minimum rainfall in this forest belt is unlikely to be less than 1000 mm per year. This medium cloud forest belt is roughly identical with the *Tsuga dumosa* forest and the upper temperate mixed broad-leaved forest described by Stainton (1972: 1–11, 98–100).

Above 3000 m the upper cloud forest of these transverse valleys is somewhat differentiated with regard to dominant tree species depending on the exposure. This is possibly caused by decreasing rainfall, which is here probably less than 1000 mm. Forest of *Abies spectabilis* still occurs on south-facing slopes (more those to the south-west than the south-east) and on wind exposed ridges on northerly slopes, whereas *Betula utilis*, which quite often forms an understory in *Abies* forests, becomes dominant on northerly slopes. *Rhododendron* thickets form the shrub layer in fir and birch forests and also, above the upper limit of *Abies* and *Betula*, dominate to form pure evergreen thickets ranging from four metres down to one metre near the timber-line, representing a transition zone from forest to alpine scrub.

In this upper cloud forest belt, branches may still be covered with mosses and ferns, but beard lichens are more frequent than in the medium cloud forest belt. On shady slopes, *Usnea longissima* is apparently more widespread and longer than on sunny slopes; branches growing out into the valleys are more densely covered with beard lichens.

Whereas birch forests and the remnants of fir forests are concentrated on the shady and sunny slopes respectively, *Rhododendron* thickets are apparently limited to those slopes which are well protected from the wind, but are not confined to any particular exposure to the sun.

The alpine belt extends from about 3400 m (owing to forest clearance) up to a maximum altitude of 5500 m and is characterized by an almost closed layer of dark alpine soil.

The most widespread plant associations between 4100 and 5500 m are dwarf shrub communities of *Rhododendron setosum*, *R. anthopogon*, and *R. nivale*, with mats of *Kobresia pygmaea*. Wind-blown and south-facing slopes up to 5000 m are dotted with dwarf prostrate junipers. The lower limit of the alpine belt is relatively clear cut on the shady slopes protected from the wind, where *Rhododendron campylocarpum* and *R. fulgens* mark the upper limit of the forest belt at about 4200 m. The sunny slopes are mostly cleared, and between 3400 and 4400 m forest and alpine species are intermixed to form the winter grazing grounds. Thus there is a transition zone of nearly 1000 m which could possibly be divided into village grazing ground and alpine pastures by the presence or absence of prostrate *Cotoneaster* spp. which are abundant around the villages.

The potential temperature limitation of the alpine belt is thought to be at about 5500 m. For the most part this is limited by other factors such as late ice melting or constant falling of frost debris from upper slopes. In the upper part of the alpine belt, the cliffs and boulders of white granite which have been free from glaciers for long enough are covered with a black carpet of lichens. Clearly the growth of lichens, even though fairly slow, occurs at a faster rate than the creation of fresh rock faces by frost action. It can therefore be assumed that with these rocks at this altitude, the process of frost cracking is negligible, a controversial conclusion because this belt has always been characterized by the dominance of periglacial processes.

In this upper alpine belt, three herbaceous communities can be distinguished on the alpine soil. The first occurs roughly between 4600 and 5000 m on sunny slopes exposed to the wind. *Kobresia pygmaea* provides about 10–30% of the plant cover, but more than 30% is covered by flat cushion-forming species such as *Anaphalis cavei*, *Leontopodium monocephalum*, *L. brachyactis*, and *Arenaria bryophylla*. In the second community, which occurs above 5000 m, *Kobresia pygmaea* covers only 5% and the area is dominated by hemispherical cushions such as

Arenaria polytrichoides, by lichens covering the dead remains of plants (one third of which are usually dead), and the dark humid soil. The third community consists of nearly 100% cover of living *Kobresia pygmaea* mats, and is confined to depressions between the valley slopes and the lateral moraines of the glaciers. These depressions are believed to be younger than the other biotopes on the evidence of the depth of the alpine soil and the diameter of the lichen *Rhizocarpon geographicum*. The problem for all these communities is that the alpine soil was obviously established by *Kobresia pygmaea*, but today this member of the Cyperaceae has nearly disappeared except in the depressions along the lateral moraines. Further research is needed to decide whether this development has coincided with a climatic change to drier or colder conditions, or if it is simply a feature of the succession that at a certain age of alpine soil cushion plants become dominant.

The lower alpine belt is typically covered by moist alpine scrub (as described by Stainton, 1972: 128). Cushions of *Rhododendron anthopogon*, *R. setosum*, *R. nivale*, and junipers with prostrate growth are characteristic of this zone and possibly represent the climax vegetation, whereas *Lonicera* spp., *Spiraea arcuata*, *Hippophae tibetana*, *Potentilla fruticosa* var *rigida*, and shrubby willows are confined to moist ravines or are part of a plant succession on moraines.

The dwarf prostrate junipers seem to prefer sunny, wind-exposed slopes, but are more frequent on the shady lee slopes when *Rhododendron setosum* and *R. anthopogon* are absent. It thus seems quite reasonable to suggest that the junipers are restricted by competition to the sunny, wind-exposed slopes.

The cushion-forming rhododendrons show a change in biotope as is explained by the ecological law of 'Relative Habitat Constancy and Changing Biotope' (Walter & Walter, 1953). At 3480 m and probably 900 mm annual precipitation, *R. setosum* occurs on sunny, wind-exposed slopes; at 4400 m its evergreen cushions are confined to wind-blown but flat sites, whereas sunny wind-exposed slopes are free from *R. setosum* and only *R. nivale* covers the steep parts of the solifluction terraces, while *R. setosum* is restricted to the shady lee slopes where the precipitation amounts to about 500 mm per year. Obviously these rhododendrons change biotopes into the ecological niche of a wind-sheltered slope, where the extra-zonal advantage compensates for the zonal disadvantages. From eco-physiological experiments carried out by Larcher (1963) with *R. ferrugineum*, it is fairly certain that the Himalayan dwarf evergreen rhododendrons are highly sensitive to frost-drought, exacerbated by wind. Thus the daily valley winds provide the limiting factor for the distribution of dwarf rhododendrons in the alpine belt, but only do so in association with temperatures below 0°C and in the absence of snow protection. During the moist summer months the rhododendrons are quite exposed to winds and form wind-deformed cushions but in winter they are protected in low ravines and other wind sheltered depressions, hence, in the alpine belt of the Khumbu Himal the distribution of dwarf rhododendron cushions, prostrate junipers, and mats of *Kobresia pygmaea* depends on exposure to the wind, as determined by micro-relief. Thus vegetation patterns in the alpine belt of these subtropical mountains at 28°N are more similar to those found in the Alps at 47°N than would be expected.

The free solifluction belt above the limit of plant cover on alpine soil extends to the maximum altitude of thawing (Kuhle, 1978) which is at about 7100 m, according to a record of a *Lecidea* sp. on the south wall of Mt Makalu (4th Jugoslavian Makalu Climbing expedition, pers. comm. J. Poelt) which must have been dependent on water. The highest records of flowering plants (species unknown) are from *c.* 6300 m on Cho Oyu (H. Heuberger, pers. comm.) and at 6350 m in the western Cwm between camps 4 and 5 by Zimmermann and Hofstetter (Zimmermann, 1954–1956) on the south side of Mt Everest. Both records refer to small cushions in crevices. This biotope provides conditions that are not typical for these altitudes, because daily movement of the substratum by thawing and freezing during the vegetative period is the most decisive limiting factor for plant colonization, but these processes are minimal in crevices densely stuffed with cushions. At the highest altitudes that I was able to find plants (5690 m) it was *Saussurea simpsoniana* that was growing in dense cushions in these crevices. Here competition is often very strong, in contrast to the surrounding free solifluction areas which are almost devoid of plants. The rather excessive movement of the substratum is only tolerated by a few specialized plants, which have shoots that lengthen with the downward creeping debris. Probably the shoot length of one growing season is approximately equivalent to the distance covered by the debris. Plants adapted to this unstable ground might be called 'solifluction acrobats' and include *Gentiana urnula*, *Eriophytum wallichii*, and *Veronica lanuginosa*. All other plants are confined to small flat patches protected from the stronger debris movement. There may occur here a nearly closed cover of plants, small cushions of crucifers, loose flat cushions of *Stellaria decumbens*, mostly with one half dead, and grasses with huge, dense root systems. Typically, their innovation buds are not at the surface, as would be expected for hemicryptophytes, but have sunk into the debris which has already moved on after the end of the growing period and are thus well protected during winter. The flora of the free solifluction belt is quite distinct from the one that occurs in patches of debris, ravines, or on gravel along streams in the alpine belt, and only a small number of species occur on both sides of the main Himalayan range.

Remarks on timber-line ecology

The striking feature of forest distribution in the valleys to the south of Mt Everest, mainly in the Khumbu Himal, is that forests predominate on the shady slopes, while the sunny slopes are covered with open woodland or grazed open pastures. In the same way, the observation that on flat ground, or on one side of ravines, forests grow higher up than on the other slope, suggests that open sunny slopes may not be favourable for forests and that this might be the result of drought. Yet one can always find solitary trees or groves on the sunny slopes. If these trees or groves do not depend on special tectonic conditions such as fault springs, which can be ruled out if the herb layer does not indicate moist conditions, one would expect woodlands or forests to occur where the topoclimatic conditions are tolerable for a single tree. The conclusion must therefore be that single trees or groves on sunny slopes are forest remnants that have survived clearances. As all these remnants are strongly influenced by grazing we do not know their natural state, but the presence of *Abies spectabilis*, *Juniperus recurva*, and *Rhododendron* spp., partly covered with *Usnea longissima*, suggests that cloud forests may be the potential vegetation, as on the shady slopes. If these conclusions are admitted, it follows that the highest altitudinal records of trees show distinct differences on different slopes. The highest altitude at which I encountered tree-forming species was over 4400 m. The very highest record was a *Juniperus recurva* south of the Ngozumpa glacier at 4440 m. It was obviously a young specimen, 60 cm tall and with a trunk diameter of 5 cm; the exposure was SSW. In the same valley and at the same exposure, I found several tree junipers between 4440 and 4420 m. The tallest were 3.5 m high with trunk diameters of 20 cm near the ground; all had been occasionally lopped. The highest grove of trees in the Khumbu Himal is situated around the houses of Pangpoche at 4240 m, with a southerly exposure. The trees are 6 m high, the diameter at breast height is 25 cm at most, and the canopy is closed. It is obviously a holy grove, with prayer flags placed on trees whose branches have not been lopped. If these highest records indicate the minimum altitude of the upper limit of forests which could then be regarded as the climatic limit, it is obvious that the potential natural and climatic upper limit of forests in the valleys south of Mt Everest, especially in the Khumbu Himal, is at least 4400 m. This height for the potential upper limit of forest is clearly applicable only to the sunny slopes; on the shady slopes, it is at least 4200 m, which coincides with the highest records for individual trees. If the tree line is higher on the sunny than the shady slopes, it can be assumed that the more favourable temperature conditions of the sunny slopes determine the difference. Thus in these valleys at the northern borders of the tropics the upper limit of forests is controlled by temperature. The rainfall is obviously not a limiting factor as an annual precipitation of as little as 500 mm, concentrated in the growing period, is enough to make the sunny slopes the more favourable ones for forests. Thus the humid parts of the Himalayas and the European Alps have similar vegetational characteristics.

This quasi theoretical upper forest line is overlain by other factors in both mountain regions. In these south-eastern parts of the Himalayas, daily cloud formation in the late morning is characteristic, with the effect that the east-facing slopes get full sun during the first four or five hours of daylight, whereas the westerly slopes are under clouds in the afternoon, when otherwise the sun would warm this exposure. At first glance it seems quite obvious that this determines the differences in the vegetation pattern of these valleys. However, there are only a few strictly east- and west-facing slopes and most are exposed to the south-east or north-east and, moreover, the south-eastern slopes are more easily accessible and more widely used for grazing and cultivation. Where strictly north-south running valleys occur, they are by contrast wooded on the eastern slopes and widely cleared on the west-facing slopes.

Another factor overlying the influences of insolation is the valley wind which occur almost daily, starting up in the late morning. The exact effect of these winds has not yet been determined, but the difference between the vegetation on wind-exposed flanks compared with that found on lee slopes is striking. Slopes mainly covered by birch forests show firs on the exposed ridges, whereas fir-covered slopes have pines on the wind-blown parts. Near the upper limit of forest, where rhododendron woodlands become dominant, exposed slopes are devoid of trees, especially rhododendrons, but dwarf rhododendron cushions (*R. setosum* and *R. anthopogon*) or dwarf prostrate junipers occur. It appears that on the wind-blown slopes, the vegetation is replaced by species that may be expected to be more drought resistant. As has been proved by experiments in the European Alps (Larcher, 1963), and with the knowledge that the growing season is undoubtedly humid while the winter is often dry and cold, one can assume that full solar radiation in winter, when the soil is frozen and water is not available, leads to transpiration rates that are significantly increased when the winds blow. This effect of seasonal drought due to freezing and enhanced by wind, probably leads to a tree-line which is naturally lower on the sunny and exposed slopes than on the shady lee slopes. As the leeward slope of a ravine in a north-south running valley is also the shady one, one can erroneously assume that the shady slope is more favourable for forests than the sunny slope.

Remarks on the influence of grazing, burning, and wood-cutting

In the area discussed there is great variation resulting from human influences. In the Barun Khola, the Iswa Khola, the Hunku Drangka, the Hinku Drangka, and the Lumding Khola, the cloud forests are in a condition which is fairly typical for the southern side of the main range. The upper cloud forest belt is cleared near the timberline for the seasonal settlements of summer grazing places. Burning is the common initial process in making clearings in order to improve the grazing conditions by the removal of the woody competitors of herbs. Usually the forests are penetrated by these clearings which are surrounded by areas of open woodland which have been gradually cleared by extensive uncontrolled grazing.

In the alpine belt there are usually summer grazing places of transhumant sheep and goats. Here the herdsmen partly burn the moist alpine scrub consisting mainly of *Rhododendron setosum*.

In the upper catchment of the Dudh Kosi, in the Khumbu Himal, the natural vegetation has been more extensively removed than is usual for this side of the Himalayas. Instead of seasonal settlements, the Sherpas have cleared the forests for the establishment of permanent settlements. Thus the influence of grazing is continuous throughout the year, in winter near the villages, in summer mainly in the lower alpine belt up to 5000 m. As the Khumbu Himal receives monsoon rains, there is relatively little snow in winter (although heavy falls may occur). For this reason, only the calves are kept in the houses during the winter and most of the cattle graze around the villages. After snowfall, the cattle at first remain in the fields near the houses, but then concentrate on grazing the slopes where the snow melts first. The influence of grazing is strongest on the south-facing 30° slopes. Steepness of slope is not a major factor governing the amount of grazing and a 10° slope close to a village is usually less grazed than a 20° slope at some distance from a village.

On these heavily grazed slopes, most of the palatable herbs other than grasses are displaced by inedible species like *Iris* spp, *Euphorbia* spp, species of Labiatae, Campanulaceae, *Gentiana* spp, orchids, and dense creeping *Cotoneaster* spp which stabilize the slopes. The duration of snow cover is a deciding factor in governing the type of vegetation. This explains partly why some forests occur on shady slopes close to the villages. Furthermore, these are to a certain extent protected by the indigenous rules of the Sherpas, who elect a forest warden whose duty is to control wood-cutting, litter collecting, and even grazing in the forest (Fürer-Haimendorf, 1964). Thanks to these laws the Sherpas have as yet no shortage of wood for fuel.

The fact that in the Khumbu Himal the natural vegetation is so largely replaced by the secondary associations is partly due to the relief. The south side of the main range is directly in contact with the Tibetan north slope and can be entered via the Nangpa-La, a pass which is only 5716 m high and is passable even for cattle. The Sherpas, who originated on the eastern slope of the Tibetan Plateau, crossed the Nangpa-La in the first half of the sixteenth century (Oppitz, 1968). It is quite probable that the original 20 to 50 settlers first practised shifting cultivation and cleared the sunny slopes by fire, while the cattle, preferring particular species such as *Abies spectabilis*, transformed the forests into open woodlands. Owing to the continually uncertain harvests the population remained small but, nevertheless, their influence on the vegetation was great because the burnt areas were invaded by *Juniperus recurva*. This species is very typical of the clearings (Stainton, 1972: 107) and, because it is not grazed by cattle, forms a comparatively stable secondary forest. Evidently there were larger forests of junipers in the Khumbu Himal in the nineteenth century. The potato was introduced into the Khumbu area about 1850 (Fürer-Haimendorf, 1964: 8). A drastic population increase followed and the juniper forests have been increasingly used for fuel, so that these secondary forests have, in turn, become open woodlands.

Alphabetical list of vascular plants, their life forms, associated formations, and records of collection

Key to plant life form symbols

The present information regarding plant life forms is based on the revised list of the Raunkiaer System of plant life forms (Ellenberg, 1956: 26) as completed by Ellenberg & Mueller-Dombois (1967).

Phanerophytes (P)
Mes P scap = large trees (5–50 m).
Mi P scap = small trees (2–5 m).
N P scap = dwarf trees (< 2 m).
Mi P caesp = tall shrubs (2–5 m).
N P caesp = normal-sized shrubs (< 2 m).
N P gram = bamboos.

Chamaephytes (Ch)
Ch frut = woody dwarf-shrubs up to 50 cm, woodiness completed into branch-tips.
Ch suff = semi-woody dwarf-shrubs. Woodiness restricted to the base of the shoot system.
Ch herb = herbaceous chamaephytes: all non-woody perennial forbs, grasses, and ferns. Most of the non-rhizoid evergreen ferns of the Khumbu area should be included here.
a = cold-deciduous (summergreen).
e = evergreen.
s = sclerophyllous.
s/e, s/a = facultatively deciduous depending on altitude, shelter from frost.
p = aphyllous (*Ephedra*).
b = needle-leaved.
rept = reptant.
pulv = pulvinate.
f pulv = flat cushions (*Silene acaulis, Gentiana acaulis*).
g pulv = globose cushions (*Androsace helvetica*).
l succ = leaf succulents dying back to shoots, some are above the ground, mostly globose-cushions.

Hemikryptophytes (H)

Remnant shoots flat on the ground, often protected by dead shoot remains. Active shoots during growing season raised above the perennial ground-shoots. Typically herbaceous, the maturing stem may be lignificated.

H caesp = branched or circular shoot system.

H rept = creeping and/or matting.
H scap = scapose without rosette.
H ros = rosette.
H sem = rosette, but with leaves on the stalk.
H scap = without rosette, mainly tall forbs.

Geophytes (G)
Survival organs protected in the soil.
G rad = root-budding geophytes.
G bulb = bulbous geophytes.
G rhiz = rhizome geophytes.
With some species information concerning the supraterrestrial growth habit is given (caesp, scap, sem, rept . . .).

Therophytes (T)
Live less than a year. Growth habit see hemikryptophytes.

Lianas (L)
PL = phanerophytic and chamaephytic lianas including all climbing plants that do not die back periodically. There are woody (frut), semi-woody (suff), and herbaceous (herb) life forms.
rPL = root climbers.
stPL = winding climbers.
elPL = tendril climbers.
dPL = spread climbers.
HL = hemikryptophytic climbers, dying periodically to a remnant shoot system near the ground.
GL = geophytic lianas, dying periodically to subterranean storage organs.
TL = therophytic lianas.

Epiphytes (E)
fac E = some phanerophytic, mainly chamaephytic woody or semi-woody facultative epiphytes, creeping on moss-covered trunks or boulders in the cloud forest belt.
obl Ch E succ = obligative epiphytes with strongly modified root system and succulent leaves.
GE bulb = bulbophytic, in moss of tree trunks.

Further morphological characteristics
rept/sem : facultatively straggling, creeping.
G rad/H sem : with storage root, sometimes shoot under the surface, sometimes near the surface.
Par : parasitic.
hyd : water plant.
fac hyd : facultatively in water (flushes, wet rocks).

In the free solifluction belt changing life forms are characteristic: without the daily moving solifluction scree most of the high altitude phanerogams would be of the hemikryptophytic or flat cushion habit. So, in flat sites, where the scree movement is little, the genetically fixed life form is typical, whereas on solifluction slopes the shoots are deformed by adapting to this movement and the plants become rhizoid.

* Drawing or colour photograph in Polumin & Stainton (1984).
+ Not included in Hara, Stearn & Williams (1978), Hara & Williams (1979), and Hara, Chater & Williams (1982).

Key to plant formation symbols

Cloud forest belt

I cloud forest (medium belt) between 2400 m/8000 ft and 3200 m/10500 ft which is altitudinally characterized by the huge *Tsuga dumosa* trees; tree-trunks and branches are moss-covered.

II open, mostly south-facing, wind-exposed grazed pine forests (*Pinus wallichiana*) up to 3500 m/11500 ft.

III cloud forest (upper belt) between 3200 m/10500 ft and the upper tree line (4200 m/13800 ft) with *Abies spectabilis*, *Betula utilis*, and *Rhododendron* thickets. Beard lichens (*Usnea longissima*) are characteristic.

IV wet, moss-covered rocks in the forest belt with species of mainly subtropical distribution (*Corallodiscus*, *Spathoglottis*) and alpine cushions (*Rhodiola*, *Saxifraga*).
V grazing grounds around the villages, with the plants originating from forest clearings and forest undergrowth, and alpine plants spreading down to the potential forest belt after deforestation.
Alpine belt
VI mostly south-facing, wind-blown dwarf juniper scrublands between 4000 m/13200 ft and 5000 m/16500 ft.
VII mostly north-facing, wind-sheltered moist alpine scrub (*Rhododendron anthopogon*, *R. setosum*, *R. nivale*) between 3800 m/12500 ft and 5200 m/17000 ft.
VIII flushes.
IX *Kobresia pygmaea* – mats between 5000 m/16500 ft and 5500 m/18000 ft.
Free solifluction belt
X phanerogams adapted to the solifluction moved scree up to the highest open slopes at about 6000 m/19700 ft.

Abbreviation list of collectors' names

The cited specimens are mainly those of the BM. The plants collected by A. Byers, J. F. Dobremez, J. Poelt, G. F. Smith, L. W. Swan, T. Wraber, and A. Zimmermann are partly cited according to duplicates in BM or determination lists which I was able to consult by the kind support of Susan Sutton (BM), Annelies Schreiber (M), Alton Byers (COLO), and George F. Smith (Stockport). Collections made after 1979 are mentioned by the date and partly by the number of collected plants and the herbarium. For further information and the collections before 1979 see Sutton (1978) and Hara, Chater & Williams (1982: 8).

B = M. L. Banerjee. Cited specimens in BM.
Beer = L. Beer. Cited specimens in BM.
BL = S. Bowes Lyon. Cited specimens in BM.
BLM = L. Beer, C. R. Lancaster, D. Morris.
By = A. Byers. Between March and November 1984, *c.* 2500 specimens. Cited according to the collector's list. The collection will be given to COLO.
D = J. F. Dobremez. Cited specimens in BM and according to the collector's list (BM).
Einarss = S. Einarssen. Cited specimen in BM.
dH. = J. de Haas. Between August and September 1974. Cited specimens in BM.
H = A. Horsfall. Cited specimens in BM.
Heub. = H. Heuberger, pers. comm. Record of *Arenaria bryophylla* between 6000 and 6100 m, Cho Oyu NE ridge, 1954.
L = Lall Dhwoj. Cited specimens in BM.
Mc = D. J. McCosh. Cited specimens in BM.
M = G. Miehe. Between August and November 1982, 318 specimens, in the BM.
N = D. H. Nicholson. Cited specimens in BM.
P = J. Poelt. Cited specimens in BM and according to the collection list compiled by A. Schreiber (M).
S = J. D. A. Stainton. Cited specimens in BM.
Sch = A. T. Schilling. Cited specimens in BM and according to collector's list (BM).
Sh = Puspa Ratna Shakya. Cited specimens in BM.
Sharma = Khadanand Sharma. Cited specimen in BM.
Sm = G. F. Smith. Between July and August 1984, above 4500 m. Cited specimens according to 'provisional list of plants . . .', typescript, Stockport, Göttingen.
Sw = L. W. Swan. Cited specimens in BM and according to collector's list (BM).
Tilman = H. W. Tilman. Cited specimen in BM.
W = T. Wraber. Cited specimens in BM and according to determination list (BM).
Z = A. Zimmermann. Cited specimens according to duplicates in BM and according to Candollea **15–17**.

Alphabetical list of flowering plants

The plant names and their authors follow *An enumeration of the flowering plants of Nepal* (Hara, Stearn & Williams, 1978; Hara & Williams, 1979; Hara, Chater & Williams, 1982).

Abies spectabilis (D. Don) Mirb.*	b Mes P scap	III	Sch.2342, W.436
Acanthocalyx nepalensis (D. Don) M. J. Cannon *	a H sem	V, VI	By.12, D.337, 380, BL.2058, 2135, M.903, Mc.322, Z.694, 1474, Sm.s.n.
Acanthopanax cissifolius (Griff. ex Seem.) Harms *	a NP caesp	I	BL.2090, Z.446, 760
Acer caudatum Wall. *	a Mi P scap	III	BL.2172, By.47, 326, 640, dH.2967, Sch.2348, 2349, 2261, 2262
A. pectinatum Wall. ex Pax *	a Mi P scap	I	S.2246, 2247, 5946
A. stachyophyllum Hiern	a Mi P scap	I	Sch.2361
Aconitum balfourii Stapf	a G bulb	V	Z.1796
A. ferox Wall. ex Seringe *	a G bulb	I, V	dH.2900, S.6577, P.s.n., P. B.78, Z.1309, 1661
A. heterophyllum Wall. ex Royle	a G bulb	V	Z.1796 A
A. hookeri Stapf *	a G bulb	V–VII	By.1132, H.50, M.1009, P.s.n., S.6595, W.196, Sm.s.n.
A. laciniatum (Brühl) Stapf var. *laciniatum*	a G bulb	V, VI	S.6577
A. rotundifolium Kar. & Kir.	a G bulb	I	P.s.n.
A. spicatum (Brühl) Stapf *	a G bulb	V	M.875, P.s.n., W.289
Aconogonum campanulatum (Hook.f.) Hara var. *campanulatum* *	a G rad	I	Z.1889
A. campanulatum var. *oblongum* (Meisn.) Hara *	a G rad	I	Z.787
A. molle (D. Don) Hara	a G rad	II, III	M.845, Z.1691A
A. rumicifolium (Royle ex Bab.) Hara *	a G rhiz	VII	D.404, P.s.n.
A. tortuosum (D. Don) Hara *	a G rad	VI	D.340, dH.1970, L.0656, Sm.s.n., Sch.2040, Z.667
Acronema cf. *hookeri* (C. B. Clarke) H. Wolff	a G rad	III, V	P.R.162
A. johrianum Babu +		?	By.993
A. tenerum (DC.) Edgew.	a G rad	VII	W.282
Aechmanthera gossypina (Wall.) Nees *	a Ch suff	I	P.69
Aeschynanthus hookeri C. B. Clarke	s obl. d E PL	I	S.4488
Agrostis munroana Aitch. & Hemsley	a H caesp	VI	P.s.n.
A. nervosa Nees ex Trin.	a H caesp	VI	M.892b, W.366a
A. pilosula var. *wallichiana* (Hook.f.) Bor	a H caesp	V	W.429
A. triaristata (Hook.f.) Bor.	a H caesp	V	W.350
Ainsliaea aptera DC. *	a H ros	VI	Z.413
Ajuga bracteosa Wall. ex Benth.	a H caesp	VI	By.893
A. lobata D. Don *	a H rept	I	Z.774
Aletris pauciflora (Klotzsch) Hand.-Mazz. *	a G rad	VI	BL.2043, By.73, D.334, 397, Z.621, 669, Sm.s.n.
Allium wallichii Kunth *	a G rad	VII, VIII	By.625, 634, 680, W.409
Alnus nepalensis D. Don *	a/e Mes P scap	I	Z.1868
Anaphalis busua (Buch.-Ham. ex D. Don) DC.	a H scap/Ch suff	I	f.M.
A. cavei Chatterjee	a f Ch herb pulv	VI, IX	M.1037, Sm.s.n.
A. contorta (D. Don) Hook.f.	a H sem	V	By.169, 314, 385, 418, 742, H.3, P.G.298

A. margaritacea (L.) Benth. *	a H sem	II	By.370, dH.2879
A. royleana DC.	a H rept/sem	II	W.303
A. tenella DC.	a H rept/sem	V	D.384, dH.2917, Z.1755
A. triplinervis (Sims) C. B. Clarke *	a H sem	V	By.411, 1130, D.332, Z.1089
A.triplinervis var. *intermedia* (DC.) Airy Shaw	a H sem	V	H.67, ?Z.s.n.
A. triplinervis var. *monocephala* (DC.) Airy Shaw *	a f Ch herb pulv/a H sem	VI	D.343, M.1015, Sm.s.n.
A. xylorhiza Sch.Bip. ex Hook.f.	a f Ch herb pulv	VI, VI, IX	H.47, BL.2110, D.414, W.210, Sm.s.n.
Andropogon munroi C. B. Clarke	a H caesp	IV	M.817b, Z.1733
Androsace delavayi Franch. *	e f Ch herb pulv	IX, X	BL.2123, Sm.s.n.
A. geraniifolia Watt	a H ros	I, IV	S.4592
A. globifera Duby *	e f Ch herb pulv	IX	D.416, Mc.323, M.1045, S.637
A. hookeriana Klatt	a H ros	VIII	Z.823
A. lehmannii Wall. ex Duby *	e g Ch herb pulv	IX	BL.2008, D.390, Mc.284, Z.816
A. nortonii Ludlow	a H ros	IX	BL.2046, By.445, D.412, Mc.318, Sm.s.n.
A. sarmentosa Wall. *	a H ros	II, V	By.46, 227, 1092, dH.2923, Z.466, 686
Anemone demissa Hook.f. & Thoms. *	a H sem	V, VII	BL.2109, D.423, Z.601, 693, Sm.s.n.
A. obtusiloba D. Don*	a H sem	III	P.R.306
A. rivularis Buch.-Ham. ex DC. *	a H sem	I, V	By.393, M.902, P.s.n.
A. rupestris Wall ex Hook.f. & Thoms.	a G bulb	I, III	BL.2087
A. rupicola Cambess. *	a G rhiz	I, III, VI, VII, VIII	S.669
Arabidopsis himalaica (Edgew.) O. E. Schulz	T sem	III, V, IX	By.121, W.297
A. lasiocarpa (Hook.f. & Thoms.) O. E. Schulz	T caesp	I, V	B.&Sh. 5656
Arctium lappa L.	a H caesp	V	f.M.
Arcyosperma primulifolium (Thoms.) O. E. Schulz	a H ros	VII	Mc.52
Arenaria bryophylla Fernald *	a g Ch herb pulv	VI, IX, X	H.33, M.1076, P.s.n., f. Heub.
A. ciliolata Edgew.	a H rept/ros	VIII, X	H.41, M.1043, Sm.s.n.
A. debilis Hook.f. ex Edgew. & Hook.f.	a H caesp	V	By.637
A. densissima Wall. ex Edgew. & Hook.f. *	a g Ch herb pulv	IX	By.797, D.410, Mc.2038, S.7115
A.edgeworthiana Majumdar	a g Ch herb pulv	VI, IX	Mc.377, W.227, Sm.s.n.
A. festucoides Benth.	a g Ch herb pulv	IX, X	Sw.s.n.
A. glanduligera Edgew. ex Edgew. & Hook.f. *	a f Ch herb pulv	VIII, X	By.385, H.28, M.955, Mc.377, P.s.n., W.178, 231, Sm.s.n.
A. glanduligera var. *cernua* N. F. Wilson	a f Ch herb pulv	VIII, X	M.1074
A. globiflora Edgew. & Hook.f.	a g Ch herb pulv	VI	BL.2073, Mc.309, S.7095
A. melandryoides Edgew. ex Edgew. & Hook.f.	a G rad/rept	IX	W.189, Sm.s.n.
A. polytrichoides Edgew. ex Edgew. & Hook.f.	a g Ch herb pulv	IX	M.989, S.7157
A. pulvinata Edgew. ex Edgew. & Hook.f.	a f Ch herb pulv	IX	By.773, Sw.s.n.

Arisaema jacquemontii Blume *	a G bulb	I	BL.2064
A. speciosum var. *mirabile* (Schott) Hara	a G bulb	I, III, V	BL.2029
A. vexillatum Hara & Ohashi	a G bulb	I	BL.2055
Artemisia biennis Willd.	a H scap	II, V	L.0181, P.G.268
A. capillaris Thunb.	a H scap	V	Z.1792
A. dubia Wall. ex Besser *	a H scap	V	Z.1655
A. indica Willd.	a H scap	V	P.s.n.
A. stricta Edgew.	a H scap	V	M.836, P.s.n., W.200, Z.1792
A. wallichiana Besser *	a H scap	VIII	B.5707, dH.2997, S.6589
Aruncus dioicus (Walter) Fernald *	a Ch suff	III	By.297, 464, Beer 25447
Arundinaria maling Gamble	a/e NP gram	I, III	W.347
Aster albescens (DC.) Hand.-Mazz. *	a H sem/Ch suff	II	M.828, Mc.392, W.361, Z.1635, 1653
A. barbellatus Grierson	a G rhiz/sem	V, VII	D.386, 415
A. diplostephioides (DC.) C. B. Clarke *	a H sem	V, VI	By.696, dH.2953a, M.899, P.R.298, Z.1717, 1822, Sm.s.n.
A. flaccidus Bunge *	a G rhiz/sem	VIII	BL.2128, D.415, Sm.s.n.
A. himalaicus C. B. Clarke *	a G rhiz	VI, IX	By.1169, M.869, 1042, Sch.2173
A. sikkimensis Hook.	a H sem/Ch suff	I	Sch.2210, 2250, Z.1880, 1885
A. stracheyi Hook.f.	a G rhiz/rept	VIII	Beer 25388, By.564, Mc.313
A. trinervius Roxb. ex D. Don *	a H sem/Ch suff	I	Z.1880a
Astilbe rivularis Buch.-Ham. ex D. Don *	a G rad	I	P.44
Astragalus chlorostachys Lindl.	a H scap	II, III	By.321, Z.1768A
A. concretus Benth.	a H rept/caesp	V	BL.2155, S.7100
A. donianus DC.	a H rept	V, VI	BL.2132, By.210, 311, 312, 339
A. floridus Benth. *	a H scap	V	S.7152
A. frigidus (L.) A. Gray	a H caesp/rept	V	P.s.n.
A. strictus Grah. ex Benth.	s Ch frut rept	V, VI	M.1013, Mc.314
Begonia picta Smith *	a/e G bulb fac E	I, IV	P.77
Berberis angulosa Wall. ex Hook.f. & Thoms. *	a NP caesp	V	Sch.2270, Z.494, 1619
B. ceratophylla G. Don	a/e NP caesp	II, V	Z.1835
B. concinna Hook.f.	a/s NP caesp	V	By.1012
B. cf. *erythroclada* Ahrendt	a/e NP caesp	V	M.992
B. jaeschkeana C. K. Schneid.	a/e NP caesp	V	By.717, 720, 967, 1112, 1154, Z.1758
B. mucrifolia Ahrendt	a Ch frut	V, VI	BL.2103
B. tsarica Ahrendt	a NP caesp	V	Z.593
B. virescens Hook.f.	a/e NP caesp	II, V	Z.480
Bergenia purpurascens (Hook.f. & Thoms.) Engl.	a G rhiz/ros	IV	By.175, Sch.2323, Z.653
Betula alnoides Buch.-Ham. ex. D. Don *	a Mes P scap	I	f.M.
B. utilis D. Don *	a Mes P scap	III	By.1157, W.434, Z.406, 492
Bistorta affinis (D. Don) Greene *	a G rhiz	VI, VII	By.478, D.365, Z.1481, Z.1573, Sm.s.n.
B. amplexicaulis (D. Don) Greene *	a G rad	V, VII	By.153, 211, M.849, 913, P.G. 348, Sch.2344

B. macrophylla D. Don) Soják *	a G rad/sem	VI, VII, IX	BL.2198, M.948, Mc.330, P.s.n., S.4521, W.201, 279, Z.737, 1478, Sm.s.n.
B. milletii Lév.	a G rad	V	W.s.n., Z.1478
B. perpusilla (Hook.f.) Greene	a G rad/rhiz	VI, IX	Beer 9552
B. vaccinifolia (Wall. ex Meisn.) Greene *	a Ch frut rept	III	By.75, 82, 137, 174, 348, 502, M.861, Sch.2346, 2175, 2181, Z.609, 1709
B. vivipara (L.) S. F. Gray	a G rad/sem	VI, VII, IX	D.366, 391, Z.640, Sm.s.n.
Biswarea tonglensis (C. B. Clarke) Cogn.	st TL	I	S.7190, Z.785
Boschniaka himalaica Hook. & Thoms. ex Hook.f. *	a G bulb	V	Mc.306
Brachyactis anomala (DC.) Kitam.	a H sem	V	M.911
Braya oxycarpa Hook.f. & Thoms. *	a G rad/H caesp/f Ch herb pulv	X	Z.564, 597
Buddleja crispa Benth. *	a NP caesp	I	Z.262
Bulbophyllum retusiusculum Reichenb.f.	obl e E Ch succ	I	L.0433
Bupleurum candollii Wall. ex DC. *	a G rad	I	D.322, P.72
Cacalia pentaloba Hand.-Mazz.	a H scap	III	B.5651, M.978
Calamagrostis emodensis Griseb.	a H caesp	?	W.394
C. epigejos (L.) Roth	a H caesp	III, V	Z.1771
C. pseudophragmites (Hall.f.) Koel. ex. Baumg.	a H caesp	VIII	Sm.s.n.
Calanthe alpina Hook.f. ex Lindl.	a G rad	I	Mc.265
Callitriche palustris L.	a hyd H caesp	IV	M.1114, P.s.n.
Campanula aristata Wall.	a H sem	V–VII	By.427, D.462, Mc.361
C. modesta Hook.f. & Thoms. *	a H scap	V	By.549, 581, L.2138, Sm.s.n.
C. nakaoi Kitam.	a G rhiz	VI, VII	S.1666, W.295
C. pallida Wall.	a H scap	V	By.307, 315, Z.1654
Capsella bursa-pastoris (L.) Medikus	T sem	V	By.214, P.78, Z.418, 1764
Cardamine inayatii O. E. Schulz +	T caesp	I, II	BL.2016
C. loxostemonoides O. E. Schulz *	a H/T scap	V	BL.2111, Mc.360
C. scutata subsp. *flexuosa* (Withering) Hara	T scap	I, II	Z.788
C. trifoliolata Hook.f. & Thoms.	T scap	I, II	Mc.272
Cardiocrinum giganteum (Wall.) Makino *	a G bulb	I	P.s.n., Sch.2248, Z.1898
Carex atrata subsp. *pullata* (Boott) Kükenthal	a G rhiz	VIII	BL.2166, D.446
C. atrofusca Schkuhr	a G rhiz	VIII	D.376, M.1094, P.G.288, R.331
C. inanis Kunth	a G rhiz/caesp	IV, VI, VIII	BL.2160
C. infuscata Nees	a G rhiz	VI, VII	M.958, 1014
C. laeta Boott	a H caesp	VI, VIII	P.R.338, Z.696
C. lehmannii Drejer	a G rhiz	VIII	P.R.121, R.325
C. munda Boott	a G rhiz/caesp	VIII	W.310
C. nakaoana T. Koyama	a H caesp	VIII	dH.2994, M.1029, P. G.219, G.292, G.297, S.666, W.169

Carpesium nepalense Less.	a H scap	III	W.397
Cassiope fastigiata (Wall.) D. Don *	s Ch frut	VII	By.469, 687, D.379, W.248, Z.612, 634, 702, 1559, 1756, Sm.s.n.
Castanopsis tribuloides (Sm.) A. DC. *	s Mes P scap	I	f.M.
Celastrus stylosus Wall.	a d LP frut	I	S.4484
Cerastium fontanum Baumg.	a H rept	?	By.498
Chamaesium novemjugum (C. B. Clarke) C. Norman	a G rad	VI, IX	M.936
Chenopodium botrys L.	T scap	V	By.724, P.s.n.
C. graveolens Willd. +		?	By.1124
Chesneya nubigena (D. Don) Ali *	a f Ch frut pulv	IX	BL.2112, By.41, M.1035, Mc.329, W.249, Sm.s.n.
Chionocharis hookeri (C. B. Clarke) J. M. Johnston *	e g Ch herb pulv	X	Sw.224, 225
Chrysosplenium alternifolium var. *sibiricum* Seringe ex DC.	H caesp/scap	IV	Z.805
C. carnosum Hook.f. & Thoms. *	H caesp	III	By.38, S.7117
C. cf. *griffithii* Hook.f. & Thoms.	a G rhiz/scap	III	M.983
C. lanuginosum Hook.f. & Thoms.	a G rhiz/sem	I, III	Z.458
C. nudicaule var. *intermedium* Hara	G rhiz/scap	VIII	BL.2035, Mc.53
Cicerbita cyanea (D. Don) Beauv.	a G rad/H scap	II	dH.2950a, P.s.n., Z.1791
C. macrantha (C. B. Clarke) Beauv. *	a Grad/H scap	V	P.s.n.
C. macrorhiza (Royle) Beauv. *	a G rad	II, V	By.586, 712, P.s.n.
C. macrorhiza var. *saxatilis* (Edgew.) Beauv.	a G rad/a H scap	IV, V	dH.2941, M.128
Circaea alpina subsp. *micrantha* (Skvortsov) Bufford +	T rept/scap	?	W.317
C. alpina subsp. *imaicola* (Aschers. & Magnus) Kitam.	T rept/scap	II	P.7
C. repens Wall. ex Aschers. & Magnus	T rept/scap	I, IV	S.5750
Cirsium falconeri (Hook.f.) Petrak *	a G rad/sem	V	W.377, Z.1670
C. verutum (D. Don) Spreng. *	a G rad/scap	V	By.601
Clematis montana Buch.-Ham. ex DC. *	a el PL frut	III	By.654, dH.2975, Sch.2186, Z.502
Clinopodium umbrosum (M. Bieb.) C. Koch	a H caesp	III	P.s.n., W.307, Z.1670
Clintonia udensis var. *alpina* (Kunth ex Baker) Hara *	a G rhiz	III	By.26, Z.641
Coccinea grandis (L.) Voigt	TL	I	P.s.n.
Codonopsis ovata Benth. *	a H scap	V	By.362
C. thalictrifolia Wall.	a G rad/rept	V–VII	By.342, 430, 453, M.1058, Sm.s.n.
Coleus barbatus (Andrews) Benth. *	a H scap/Ch suff	II	Z.1833, 1865
Colutea multiflora Shap. *	a NP caesp	I, II	dH.2951, Sch.2165
Commelina paludosa Blume *	a H scap	II	By.465
Corallodiscus lanuginosus (Wall. ex DC.) Burtt *	e H ros	IV	D.321, Mc.394, M.811, Z.422, 1225
Cortia depressa (D. Don) C. Norman *	a G rad	VI, IX	BL.2179, D.368, P.s.n., G.259, Sm.s.n.

Cortiella hookeri (C. B. Clarke) C. Norman *	a G rad	IX, X	M.1001, W.164, 233, Sm.s.n.
Corydalis cashmeriana Royle *	a G bulb	V, VII	D.431, Mc.283, P.s.n.
C. casimiriana Prain		V	H.10 (f. Lidén)
C. cavei D. G. Long		V	H.10 (f. Lidén)
C. chaerophylla DC.		I	Mc.266
C. chasmophila Ludlow	a H caesp	VII	BL.2163, S.628
C. flabellata Edgew.		?	By.193
C. flaccida Hook. f.& Thoms.		III	Mc.295, S.8360
C. govaniana Wall. *	a H caesp	III, V	M.879, Z.809, Sm.s.n.
C. hookeri Prain		VII	S.7153
C. juncea Wall. *	a G bulb/scap	III, V	BL.2164, Mc.341, S.4538
C. leptocarpa Hook.f. & Thoms.		III	S.4536
C. longipes DC.	a G rad/caesp	III	By.525, 1167, dH.2935, M.850, W.386
C. meifolia Wall. var. *meifolia* *	a H caesp	VII	M.1083, Beer 9555, Sm.s.n.
C. polygalina Hook.f. & Thoms.	a G bulb	VII	Mc.327
C. stracheyi Duthie ex Prain +	a H caesp	VI	D.357
Corylus ferox Wall. *	a Mes P scap	I	S.4606
Cotoneaster acuminatus Lindl.	a N P caesp	II, V	dH.2930, M.854, Mc.273, S.4614, Sch.2030
C. adpressus Bois	a Ch frut rept	II, V	Sch.2031, 2263
C. frigidus Wall. ex Lindl. *	a Mi P caesp	II	Sch.2442A
C. integrifolius (Roxb.) Klotz	s Ch frut rept	II, V	S.7125
C. meuselii Klotz	a N P caesp	II	Sch.2355
C. microphyllus Wall. ex Lindl. *	s Ch frut rept	V	By.1089, P.s.n., Sch.2032
C. nitidus Jacques	s/a N P caesp	II, V	M.932
C. sanguineus Yü	a N P caesp	II	Mc.304, BL.2168
Cremanthodium decaisnei C. B. Clarke *	a H ros	VIII, X	BL.2121, Mc.371, Sm.s.n.
C. ellisii (Hook.f.) Kitam. *	a H ros	VIII, X	M.1108, W.165, Z.1456B, Sm.s.n.
C. nepalense Kitam. *	a H ros	VII	By.592, H.46, Sm.s.n.
C. oblongatum C. B. Clarke *	a H ros	VII, X	By.545, M.901, 966, Z.1471
C. reniforme (DC.) Benth. *	a H sem	VII	By.506, 639, M.895, Z.1451
C. retusum (Wall. ex Hook.f.) R. Good *	a H sem	VII	Z.1451
Crepis tibetica Babcock	a H ros/sem	?	W.299
Cryptothladia polyphylla (Wall. ex DC.) M. J. Cannon *	a G rad	V, VII	Mc.381
Cuscuta reflexa Roxb.	ELT Par	II	P.s.n.
Cyananthus hookeri C. B. Clarke	a H rept	V, VI	H.17, 53, M.831, 915, W.206
C. incanus Hook.f. & Thoms. *	a G rad/H rept	V, VI	By.76, 299, 328, 678, 1082, dH.2943, W.238, Z.1648, 1714, Sm.s.n.
C. inflatus Hook.f. & Thoms.	a H rept/scap	V	By.492, H.9, M.914, P.85, 88
C. lobatus Wall. ex Benth. *	a G rad/H rept	V	P.89
C. microphyllus Edgew. *	a G rad/H rept	V	H.5, 55, P.94
C. pedunculatus C. B. Clarke	a H rept	V, VI	By.587, 795, M.873, P.s.n.
C. spathulifolius Nannfeldt	a G rad/rept	VI, VII	Mc.308
Cyanotis vaga (Lour.) J. A. & J. H. Schultes *	a H	II	By.466
Cymbidium hookerianum Reichenb. f. *	fac. e Ch E succ	I	S.4476

Cynanchum auriculatum Wight	a d PL frut	I	Mc.395
Cynoglossum glochidiatum Wall. ex Benth. *	a H scap	II, V	B.5659, Mc.275, P.193
C. zeylanicum (Vahl) Thunb. ex Lehm.	a H scap/caesp	II, V	By.397, 872
Cypripedium himalaicum Rolfe apud Hemsl. *	a G rhiz	VII	BL.2199, By.120, D.395, Sm.s.n.
Dactylorhiza hatagirea (D. Don) Soó *	a G rad	V	By.142
Danthonia cachemyriana Jaub. & Spach	a H caesp	V	M.892c, P.s.n.
D. cumminsii Hook.f.	a H caesp	I	M.877, 851b, W.349
Daphne bholua Buch.-Ham. ex D. Don	s NP caesp	I	S.4480
D. retusa Hemsl. *	s NP caesp	I	W.328
Datura stramonium L. *	a H scap	V	f.M.
Delphinium caeruleum Jacquem. ex Cambess.	a H sem	II, V	P.s.n.
D. drepanocentrum (Brühl) Munz *	a H sem	V	By.423, 537, 621, dH.2969, L.0191, M.882
D. glaciale Hook.f. & Thoms.	a H sem	X	M.1060, P.s.n., W.172, 219, Sm.s.n.
D. cf. *nepalense* Kitam. & Tamura	a H sem	VII	M.1033
D. viscosum Hook.f. & Thoms. *	a H sem	VII	Beer 25387, W.372
Desideria nepalensis Hara		X	Sw.71–72
Desmodium elegans DC. *	a NP caesp	II	By.364
D. heterophyllum (Willd.) DC.	a NP caesp	II	P.s.n.
Deutzia bhutanensis Zaikonn. *	a NP caesp	II	Mc.38, S.4621
D. compacta Craib *	a NP caesp	II	BL.2157, By.499, S.7123
D. staminea R. Br. ex Wall. *	a NP caesp	II	Sch.2087, Z.472, 1860, s.n.
Deyeuxia pulchella (Griseb.) Hook.f.	a G rhiz	III, V–VIII	M.817, 817a, 1021b, 1028, W.247
Dicentra scandens (D. Don) Walp.	a d HL	II	P.s.n., Z.1883
Dichrocephala benthamii C. B. Clarke	a H sem	I, II	Z.749B
D. integrifolia (L.f.) O. Kuntze	a H sem	II	Z.749
Didymocarpus aromaticus Wall. ex D. Don	a G bulb/scap	IV	Z.746
D. oblongus Wall. ex D. Don	a G bulb/scap	IV	S.7163
D. primulifolius, D. Don *	a G bulb/scap	IV	S.7164
Diphylax urceolata (C. B. Clarke) Hook.f.	a G rad	IV	L.0529
Diplarche multiflora Hook.f. & Thoms.	s Ch frut/rept	III	Beer 25361, Sw.441
Dipsacus inermis var. *mitis* (D. Don) Y. Nasir	a H sem/scap	I, III	Z.1671
Disporum cantoniense (Lour.) Merr. *	a G rad/scap	II	Z.765
D. cantoniense var. *parviflorum* (Wall.) Hara	a G rad	II	Sch.2366A
Dodecadenia grandiflora Nees *	s Mes P scap	I	S.6559
Draba altaica (C. A. Meyer) Bunge *	a H ros/a f Ch herb pulv	X	Mc.325, W.167
D. amoena O. E. Schulz *	a H sem	V	BL.2178, D.424. S.7144
D. elata Hook.f. & Thoms.	a H sem	VII, VIII	BL.2114, D.440, Mc.287, Z.521, 581

D. ellipsoidea Hook.f. & Thoms.	T caesp	V	W.204
D. gracillima Hook.f. & Thoms.	T sem	V, VII	Z.807
D. lasiophylla Royle	a f Ch herb pulv/a H ros	IX, X	BL.2075, M.1102, Sm.s.n., S.7158, W.175, 184
D. lasiophylla var. *leiocarpa* (Pamp.) O. E. Schulz	a f Ch herb pulv	VI, VII	D.445
D. cf. *oariocarpa* O. E. Schulz	a H ros/a f Ch herb pulv	VII, IX	P.G.206
D. oreades Schrenk *	a H ros/a f Ch herb pulv/G rhiz	X	BL.2190, M.1098, Z.569
Drosera peltata Smith	a H ros	III, V	By.365, D.333, Z.1694
Drymaria cordata (L.) Willd. ex Roem. & Schult.	a H rept/a f Ch herb pulv	IX, X	BL.2119
Dubyaea hispida DC. *	a H scap/G rad	V, VI	By.583, 590, 591, dH.2962, M.880, P.s.n., W.330, Z.s.n.
Elaeagnus infundibularis Momiyama	a/e Mes/Mi P scap/caesp	I	P.s.n., Sch.2442A, S.6574, Z.1850
Elsholtzia concinna Vautier	T scap/caesp	II, V	Z.1778
E. densa Benth.	a H scap	V	Z.683
E. eriostachya (Benth.) Benth. *	T scap	II, V	By.205, 675, D.339, L.0180, M.889
E. eriostachya var. *pusilla* (Benth.) Hook.f.	T scap	II, V	Z.643
E. fruticosa (D. Don) Rehder *	a NP caesp/Ch suff	II	By.509, 611, 882, 1123, M.822, P.s.n., Z.1654, 1828
E. strobilifera (Benth.) Benth.	T scap	II, III	M.889a, P.s.n., W.302, Z.1726
Elymus canaliculatus (Nevski) Tzvel.	a H caesp	V, VI	M.851a
E. nutans Griseb.	a H caesp	VI	P.s.n.
Enkianthus deflexus (Griff.) Schneid. *	s/a Mi P caesp	I	BL.2013, Sch.2336, Z.426
Ephedra gerardiana var. *sikkimensis* Stapf *	p Ch frut	II, V, VI, IX	By.736, BL.2069, D.439, M.993, P.R.333, G.293, Sch.2102, W.258, Sm.s.n.
Epilobium conspersum Hausskn.	a H scap	V, VI	By.310, P.R.336
E. leiospermum Hausskn.	a H scap	?	W.384, 392
E. cf. *wallichianum* Hausskn. *	a H scap	IV, VIII	M.844
E. williamsii Raven		?	W.300
Erigeron bellidioides (Buch.-Ham. ex D. Don) Benth. ex C. B. Clarke *	a H sem	II	D.325, Z.447, 451, 727
E. kumaunensis (Vierh.) Wendelbo	a H sem	II, V	Z.1864
E. multiradiatus (Lindl. ex DC.) C. B. Clarke *	a H sem	V, VI	By.294, M.876, Z.451, 1565, 1622
Eriophyton wallichii Benth. *	a G rhiz/scap	X	By.1173, M.1007, W.236, Z.1510, Sm.s.n.
Erysimum hieraciifolium L.	T scap	II, V	Z.450
Euonymus amygdalifolius Franch.	s NP caesp	I	S.6573
E. frigidus Wall.	s NP caesp	I	P.s.n.
E. hamiltonianus Wall. *	a Mi P scap	I	By.988
E. pendulus Wall.	s Mes P scap	I	S.6572
E. porphyreus Loesener +	a Mi P scap	I	Mc.43, S.5949

E. tingens Wall. *	s Mi P scap	I, III	S.4607
Euphorbia himalayensis Klotzsch	a G rad/scap	II, V	Sch.2086, 2291, 2324
E. longifolia D. Don	a G rad/scap	II, V	Sch.2069
E. pseudosikkimensis (Hurusawa & Ya. Tanaka) Radcliffe-Smith	a G rad/scap	II, V	dH.2959
E. sikkimensis Boiss.	a G rad/scap	II, V	Sch.2060
E. stracheyi Boiss.	a G rad/rept	V, VI, IX	B.5698, BL.2131, M.954, Z.490, 410, 537, Sm.s.n.
E. wallichii Hook.f. *	a G rad/scap	II, V	By.101, 1127, M.826, Z.378
Euphrasia himalayica Wettst. *	T scap	VIII, IX	By.415, Sm.s.n.
E. platyphylla Pennell	T scap	VII	S.656
E. secundiflora Pennell	T scap	V	P.s.n.
Eurya acuminata DC. *	s Mes P scap	I	S.4482
Fagopyrum dibotrys (D. Don) Hara	a H sem	II	Z.766, 1862
F. esculentum Moench	a H scap	V	By.304, 701
Festuca ovina L.	a H caesp	VI	Mc.289, W.183, 242, Sm.s.n.
F. polycolea Stapf	a H caesp	VI, VII	D.373, S.550
Festuca tibetica (Stapf) Alexeev +	a H caesp	X	M.1072
Ficus sarmentosa Buch.-Ham. ex Sm.	s r PL frut	I, IV	f.M.
Fragaria nubicola Lindl. ex Lacaita *	a H caesp	V	By.1129
Fritillaria cirrhosa D. Don	a G bulb	III, V, VII	Z.690, Sm.s.n.
Galearis stracheyi (Hook.f.) P. F. Hunt *	a G rhiz	VI, VII	By.131, D.427
Galinsoga parviflora Cav.	T scap	V	Z.1765
Galium aparine L. var. *aparine*		III, V	By.636, P.s.n.
G. asperifolium Wall.	T rept	III	W.426
G. asperifolium var. *sikkimense* (Gandoger) Cufodontis	T rept	IV	P.R.275
G. asperuloides subsp. *hoffmeisterii* (Klotzsch) Hara	T rept	III, V	W.306
Gaultheria fragrantissima Wall. *	s NP caesp	III	Sch.2050, Z.444, 1856
G. hookeri C. B. Clarke	s NP caesp	III	BL.2022, S.4612
G. nummularioides D. Don	s Ch frut rept	I	M.820
G. pyroloides Hook.f. & Thoms. ex Miq. *	s Ch frut rept	III	S.4616, Z.792
G. trichophylla Royle *	s Ch frut rept	III	By.109, M.970, S.4541, Z.623, 1785
Gentiana algida Pall. *	e H caesp/rept	VIII	S.6591
G. algida var. *nubigena* (Edgew.) Kusn.	e H rept/sem	VIII	M.1075, P.G.203, Sch.2313, Sm.s.n.
G. algida var. *parviflora* (C. B. Clarke) Kusn.	e H rept	VIII	Sm.s.n.
G. algida subsp. *przewalskii* (Maxim.) Kusn.	e H rept/sem	VIII	H.49
G. argentea (D. Don) C. B. Clarke	e H scap	II, III	E. Onyon 5
G. capitata Buch.-Ham. ex D. Don *	e H ros	III	Sw.525
G. crassuloides Bur. & Franch.	e H caesp	?	Sm.s.n.
G. depressa D. Don *	e f Ch herb pulv	V	By.362, H.56, M.1117, P.147, 149, Sch.2316, Tilman s.n.

G. elwesii C. B. Clarke	a H sem	VII	Beer 25368
G. infelix C. B. Clarke	a H caesp	VIII	BLM 9548
G. ludlowii Marq.	e H sem/caesp	V, VI, VIII	H.2, 25, M.940, P.R.291
G. micans C. B. Clarke	e H sem/caesp	V	dH.2963, Sm.s.n.
G. ornata (G. Don) Griseb. *	e H caesp/sem/e f Ch herb pulv	V, VI	By.597, H.35, M872, P.R.290, G.212, S.1673, 6587, Sch.2314, Sharma E.465, W.220, Sm.s.n.
G. ornata forma alba	e f Ch herb pulv	VI	M.1082
G. pedicellata (D. Don) Griseb. *	H caesp	V	Sw.428
G. phyllocalyx C. B. Clarke *	a H sem/G rhiz	V, VI, IX	S.589
G. prolata Balf.f.	e H caesp/rept	V	Sch.2184
G. sikkimensis C. B. Clarke	a H scap	?	W.158
G. speciosa (Wall.) Marq.	a H rept	I, II	P.B.9, 153, 154, Sch.2081
G. squarrosa Ledeb. +		VI, IX	D.2996, P.s.n.
G. stellata Turrill +	a H sem/caesp	VI	P.G.287, S.1674, 1694, W.239
G. strobilacea H. Sm.	e H ros	VII	Sw.314
G. tubiflora (G. Don) Griseb. *	e H ros	IX, X	BLM 9549
G. urnula H. Sm. *	e H ros/G rhiz	X	M.1080, Sch.2314, S.6595, Sw.21–23, Sm.s.n.
G. vernayi Marq.	T caesp	V, VII, IX	H.24, M.1088, W.205
Gentiana sp.	a H ros	X	M.1088
Gentianella falcata (Turcz. ex Kar. & Kir.) H. Sm.	T ros/sem	VI, IX	M.999, P.R.334, G.253, G.302, Sm.s.n.
G. glanduligera Airy Shaw	a H ros/sem	?	W.427
G. pedunculata (D. Don) H. Sm.	T sem/scap	IX	M.1110, P.s.n., W.221
G. stellariifolia (Franch. ex Hemsl.) H. Sm.	T caesp	VI, VII	S.1677
Geranium donianum Sweet *	a H sem	VII	By.14, 152, D.335, 401, M.947, S.7150, Sm.s.n.
G. nakaoanum Hara *	a H ros	VII	By.1146, D.360, Sm.s.n.
G. polyanthes Edgew. & Hook.f. *	a H sem	V	By.275, P.G.329
G. refractum Edgew. & Hook.f. *	a H sem	VII	By.192, 234, 463, BL.2096, D.420, H.37, Mc.347, Sm.s.n.
Gerbera maxima (D. Don) Beauverd var. *maxima*	a H sem/G rad	II	Z.1872
G. nivea (DC.) Sch. Bip.	a G rad/H ros	V	By.670, 787, P.s.n., W.353
Girardinia diversifolia (Link) Friis *	a H scap	II	Z.1874
Goodyera fusca (Lindl.) Hook.f.	a G rad/rhiz	III	M.925, W.316
G. repens (L.) R. Br. *	a G rhiz	III	By.642
Gueldenstaedtia himalaica Baker *	a G rad/H caesp	V–VII	By.268, BL.2065, D.345, H.32, Mc.321, Sm.s.n.
Gymnadenia orchidis Lindl.	a G rad	V–VII	L.0193
Gypsophila cerastioides D. Don *	a H rept/a f Ch herb pulv	VIII	By.316, BL.2165, M.979, Mc.344
Habenaria arietina Hook.f.	a G bulb	II, III, V	H.70
Hackelia uncinata (Royle ex Benth.) C. E. C. Fischer	a H scap	III, V	BL.274
Halenia elliptica D. Don *	T sem	V	By.239, 431, M.918, W.294
Hedera nepalensis K. Koch	s r PL frut	I, III	Z.1838, 1840
Hedychium densiflorum Wall.	a G bulb	I, II	Sch.2042
H. spicatum Smith *	a G bulb	I, II	Sch.2043
Hedysarum sikkimense Benth. ex Baker *	a H rept	V–VII	BL.2079, By.43, 438, M.1024, Mc.310, S.7101, Sm.s.n.

Helictotrichon sp.	a H caesp	V	M.892
Hemiphragma heterophyllum Wall. *	a H rept	III	dH.2978, Z.1819
Heracleum brunonis (DC.) C. B. Clarke	a G rad	?	By.322, 345
H. candicans Wall. ex DC.	a G rad	I, III, V	BL.2150, By.850, S.6598
H. nepalense D. Don	a G rad	III, V	M.883b
H. wallichii DC.	a G rad	III, V	By.809, M.883c
Herminium josephii Reichenb.f.	a G bulb	VI, VII	D.393
H. lanceum (Thunb.) Vuijk *	a G bulb	V	H.65a
H. macrophyllum (D. Don) Dandy	a G bulb	V	BL.2174, M.945, Mc.311
H. pugioniforme Lindl. ex Hook.f.	a G bulb	V	Mc.355
Hierochloe flexuosa Hook.f.	a H caesp	?	By.520
Hippophae tibetana Schlecht. *	a/e Ch frut/pulv	VIII	By.428, dH.2989, f.M., P.G.305, f.Sch.(2268), 2179
Holboellia latifolia Wall.	a el PL frut	I, II	S.4490
H. latifolia var. *angustifolia* (Wall.) Hook.f. & Thoms. *	a el PL frut	I, II	Z.432, 473
Hydrangea heteromalla D. Don	a Ch frut/r PL frut	I	Mc.269
Hypecoum leptocarpum Hook.f. & Thoms.	a H caesp/rept	VII, VIII	By.768, Sm.s.n.
Hypericum choisianum Wall. ex N. Robson *	a H caesp	II	Mc.399, S.7168
H. himalaicum N. Robson	a H scap	II	Mc.404
Ilex dipyrena Wall. *	s Mi P scap	I	Z.1675
I. intricata Hook.f.	s NP caesp	III	P.73, S.4611
I. odorata Buch.-Ham. ex D. Don	s Mi P scap	III	S.4610
I. sikkimensis Kurz	a Mi P scap	I	BL.2019
Impatiens falcifer Hook.f.	a H caesp	?	By.246, 376
I. glandulifera Royle *	T scap	II, V	By.665
I. puberula DC.	a H scap	I, IV	D.328
I. pulchra Hook.f. & Thoms.	a H scap	I, IV	L.067
I. sulcata Wall. *	a H scap	I, IV	By.300, 573–575, W.341
I. urticifolia Wall. *	a H scap	V	f.M.
Indigofera bracteata Grah. ex Baker	a H caesp	II	D.326
I. heterantha Wall. ex Brandis *	a NP caesp	II	S.4622
Inula cappa (Buch.-Ham. ex D. Don) DC. *	a/e Ch suff	II	Z.1881
I. hookeri C. B. Clarke *	a H scap	II	dH.2916, P.s.n., S.6570, Z.1693, 1845A
I. nervosa Wall. ex DC.	a/e G rhiz/H scap	II	dH.2919
Iris kemaonensis D. Don ex Royle *	a G rhiz	V	By.81
Jasminum humile L. *	s d PL frut	II	dH.2913, Z.666
J. humile forma *pubigerum* (D. Don) Grohmann	s d PL frut	II	By.860
J. humile var. *revolutum* (Sims) Stokes	s d PL frut	II, V	P.G.203
Juncus benghalensis Kunth	a G rhiz	IV, VIII	P.R.327
J. clarkei Buchenau +	a G rhiz	?	W.322
J. concinnus D. Don	a G rhiz	IV	M.868, P.B.55, 171
J. grisebachii Buchenau	a G rhiz	?	W.376
J. himalensis Klotzsch *	a G rhiz	VIII	M.1029a, S.567
J. leschenaultii Gay	a H caesp	IV	Z.1724

J. leucanthus Royle ex D. Don *	a G rhiz	IV	By.285, D.409, M.956, W.188a, 252, Sm.s.n.
J. leucomelas Royle ex D. Don *	a H caesp	VIII	D.409
J. pseudocastaneus (Lingelsh.) Samuelsson	a G rhiz	?	By.546
J. sphacelatus Decaisne	a G rhiz	VIII, X	D.377, M.1093, P.R.326
J. thomsonii Buchenau	a G rhiz	III, IV	By.222, P.G.264, S.7096, W.188, 190, Z.665, 1524, 1540
Juniperus indica Bertol. *	b N/Mi P scap/Ch frut	III, V, VI	By.1134, D.459, P.G.300, 318, S.4513, 4515, 4528, 7116
J. recurva Buch.-Ham. ex D. Don *	b N/Mi P scap	III, V	By.80, P.3, 4, S.4529, 4514, W.410
J. squamata Buch.-Ham. ex D. Don *	b Ch frut/rept	VI	By.1168, Z.1699
Kobresia caricina Willd.	a H caesp	VIII, X	BL.2127
K. curvata Kükenthal	a H caesp	IV	M.867, P.132
K. deasyi C. B. Clarke		VIII, X	P.G.267
K. fissiglumis C. B. Clarke +	a H caesp	?	W.269
K. macrantha Boeck.	a H caesp	VIII, X	BL.2188
K. nepalensis (Nees) Kükenthal	a H caesp	VI, VIII, IX, X	M.s.n., 959, 988, 1071a
K. pygmaea (C. B. Clarke) C. B. Clarke	a H caesp	IX	M.957, 1071b, P.R.332, W.237
K. schoenoides (C. A. Meyer) Steudel	a H caesp	VIII, X	M.1053, 1104, 1111
K. seticulmis Boeck.	a H caesp	IV, VI, VII, X	M.866, 1087, Mc.2032, P.133, 134, R.226
K. trinervis Boeck.	a H caesp	VI	BL.2197
Koenigia delicatula (Meisn.) Hara	T rept	IV	M.916, P.s.n., W.382
K. islandica L.	T rept	VIII	W.245, Z.651
K. nepalensis D. Don	T rept	VIII	M.981, Mc.312, W.381
Lactuca lessertiana (DC.) C. B. Clarke *	a H sem/G rad	III, VI, VII	M.982, 1023, W.251, Z.1529, Sm.s.n.
Lagotis kunawurensis (Royle ex Benth.) Rupr. *	a H ros	VIII, X	BL.2105, By.392, D.407, M.1069, Sm.s.n.
Lamium nepalense Hedge	a H scap	II	L.0139
Lancea tibetica Hook.f. & Thoms. *	a H ros	VI	BL.2117, By.13, D.442, Sm.s.n.
Lasiocaryum densiflorum (Duthie) J. M. Johnston	T caesp	VI, IX	By. 668
L. diffusum (A. Brand) J. M. Johnston	T caesp	VI, IX	W.208
L. munroi (C. B. Clarke) J. M. Johnston	a H sem	?	Beer 25543
Leibnitzia nepalensis (Kunze) Kitam.	a H ros	V	Z.403
L. ruficoma (Franch.) Kitam.	a H ros/G rad	V	dH.2945, Z.1754
Leontopodium brachyactis Gand.	a H sem/f Ch herb pulv	V, VI	M.881, 942, W.403
L. jacotianum Beauverd *	G rhiz/ros/sem	VI	D.356, Z.1607, 1697, Sm.s.n.
L. monocephalum Edgew.	a f Ch herb pulv	IX	BL.2139, D.428, H.48, M.1048, 1068, 1092, P.G.207, G.257, S.6582, W.166, Z.1591, Sm.s.n.

L. nanum (Hook.f. & Thoms. ex C. B. Clarke) Hand.-Mazz.	a f Ch herb pulv	IX	BL.2125, M.1041
L. stracheyi (Hook.f.) C. B. Clarke ex Hemsley	a H caesp	II	By.389, dH.2953, M.833, P.111, 112, Sch.2176, Z.1651, 1821
Lepidium capitatum Hook.f. & Thoms.	T rept	IX	M.1116
Leptodermis kumanoensis Parker *	a NP caesp	III	S.7160
L. stapfiana H. Winkler	a NP caesp	II	S.4618
Leucosceptrum canum Sm. *	a NP caesp	II	Z.1858
Leycesteria formosa Wall. *	a NP caesp	II	P.96, Z.743
Lignariella hobsonii (Pearson) Baehni *	T rept	VIII	W.331
L. hobsonii subsp. *serpens* (W. W. Smith) Hara	T rept	V	BL.2207
Ligularia amplexicaulis DC. *	a H sem	III, V	By.171
L. fischerii (Ledeb.) Turcz. *	a H scap	II, V	By.286, L.0182
Lilium nanum Klotzsch *	a G bulb	II, V	BL.2056, 2074, By.150, S.4775
L. nepalense D. Don *	a G bulb	I, II, V	By.176, 179, Sch.2248
Lindera heterophylla Meisn.	s Mes P scap	I	S.6566
L. neesiana (Wall. ex Nees) Kurz	a/s Mes P scap	I	S.6571, 6599
L. pulcherrima (Nees) Benth. ex Hook.f. *	a/s Mes P scap	I	Z.260
Listera nepalensis Balakrishnan	a G rad	?	W.339
Litsea cubeba (Lour.) Pers.	a Mes P scap	I	S.6567
L. sericea (Wall. ex Nees) Hook.f.	s Mes P scap	I	S.5942
Lloydia flavonutans Hara	a G bulb	V	Mc.279
L. longiscapa Hook *	a G bulb	V	Beer 25375, Sm.s.n.
L. serotina (L.) Reichenb. *	a G bulb	VI, VII	BL.2962, By.308, D.375
L. serotina var. *parva* (Marquand & Shaw) Hara	a G bulb	VI	BL.2170, M.944, Mc.326
Lobelia seguinii H. Lév. & Van.	a H scap	II	Z.1863
Lomatogonium brachyantherum (C. B. Clarke) Fernald	a H caesp	VIII, IX	H.34, P.R.347
L. carinthiacum (Wulf.) Reichenb. *	a H sem	VI–IX	By.1174, M.1056, P.G.223, R.329, S.6593, W.250
L. chumbicum (Burkhill) H. Sm.	a H sem	VI	M.946, W.402
L. graciliflorum H. Sm.	a H sem	?	W.292, 400
L. sikkimense (Burkhill) H. Sm.	a H sem	V	W.420
Lonicera acuminata Wall.	a Ch frut	II	Mc.393
L. angustifolia Wall. ex DC.	a Mi P caesp	III	BL.2083, 2152, By.68, 873, M.935, Z.429
L. cyanocarpa var. *porphyrantha* Marquand & Shaw *	a Ch frut	VII	Mc.305
L. hispida Pall. ex Willd. *	a NP caesp	VI, VII	D.434, Sm.s.n.
L. hispida var. *setosa* Hook.f. & Thoms.	a Ch frut	VI, VII, IX	BL.2104, M.1050, Mc.350
L. lanceolata Wall.	a NP caesp	III	BL.2023, By.51, 282, 557, 1002, D.452, M.934
L. litangensis Batalin	a Ch frut	VI, VII	Z.520
L. myrtillus Hook.f. & Thoms. *	a Ch frut	VI, VII	By.425, D.418
L. obovata Royle ex Hook.f. & Thoms. *	a Ch frut	V–VII	BL.2185, By.903, P.R.357, Sch.2078, Z.614, Sm.s.n.
L. rupicola Hook.f. & Thoms. *	a Ch/NP caesp	III, V	By.37, M.985, P.R.358, Z.509, 1530, Sm.s.n.
Luzula sp.	H caesp	III	P.R.341

Lyonia ovalifolia (Wall.) Drude *	a/s N/Mi P scap	III	f.M.
L. villosa (Hook.f.) Hand.-Mazz. *	a/s N/Mi P scap	III	M.858, P.G.358, Z.1852
Lysimachia prolifera Klatt	a H caesp/rept	I, III	Z.781
Malaxis cylindrostachya (Lindl.) Kuntze	a G bulb	II, V	Mc.397
M. muscifera (Lindl.) Kuntze	a G bulb	V	By.332, H.15
Mandragora caulescens subsp. *flavida* Grierson & Long *	a G rad/ros	V	Z.688
Meconopsis bella Prain *	a H scap	III, V	Beer 25425, BL.2161
M. horridula Hook.f. & Thoms. *	a H sem	V–VII, IX	By.451, H.51, P.s.n., Sch.2177, 2351, W.280, Sm.s.n.
M. paniculata Prain *	a H sem	III, V	S.649, W.395
M. simplicifolia (D. Don) Walp *	a H scap	III, VII	By.28, Mc.348, Z.594
M. sinuata Prain *	a H scap	VII, VIII	Beer 25445
Megacodon stylophorus (C. B. Clarke) H. Sm. *	a H scap	III, V	BL.2153, By.271, L.0183, Z.1703
Meliosma dilleniifolia (Wall. ex Wight & Arn.) Walp.	a Mi P scap	I	S.4620
Michelia doltsopa Buch.-Ham. ex DC. *	s Mes P scap	I	S.4478
Microcaryum pygmaeum (C. B. Clarke) J. M. Johnston	T ros	V, VI, IX	M.s.n.
Micromeria biflora (Buch.-Ham. ex D. Don) Benth. *	a H caesp	II	Z.400
Microsisymbrium axillare (Hook.f. & Thoms.) O. E. Schulz	a H sem	II, V	Z.258
Microula pustulosa (C. B. Clarke) Duthie	a H caesp/scap	V, VI	BL.2156
M. sikkimensis (C. B. Clarke) Hemsl. *	a H scap	V	BL.2183, D.367, M.887, Sm.s.n.
Miscanthus nepalensis (Trin.) Hackel	a H caesp	II	Sch.2063, Z.1859
Myricaria davurica (Willd.) Ehrenb.	s Ch frut	VIII	Z.510
M. rosea W. W. Sm. *	s Ch frut rept	VIII	By.350, dH.2971, M.969, P.s.n., Sm.s.n., W.432
Nannoglottis hookeri (C. B. Clarke ex Hook.f.) Kitam. *	a H scap/G rad	III	By.220, Einarsson 9, L.0178, M.870, Mc.444, P.s.n., S.3820, 7130, Z.635, 687
Nardostachys grandiflora DC. *	a H sem	V, VI	L.0212
Neilla rubiflora D. Don	a NP caesp	II	BL.2081
Neolitsea pallens (D. Don) Momiyama & Hara ex Hara *	s Mi P scap	I, II	S.4482
Neottianthe calcicola (W. W. Smith) Schlechter	a G bulb	II, V, VII	H.26, M.963, P.16
N. secundiflora (Hook.f.) Schlechter	a G bulb	II, V	H.61, P.16
Nepeta coerulescens Maxim.	a H scap	V	B.5778
N. lamiopsis Benth. ex Hook.f.	a H rept/scap	V	B.5636, By.52, D.385, H.16, L.0170, M.905, Mc.359, P.s.n., Z.1766
Notholirion macrophyllum (D. Don) Boiss. *	a G rad	III, V–VII	By.217, D.331, Sch.2105

Omphalodes trichocarpa Maxim. +		?	By.41, 213, 374, 892
Orchis diantha Schlechter +	a G rhiz	V, VI	Mc.294, BL.2048
Oreorchis foliosa (Lindl.) Lindl. *	a G bulb	I	BL.2026, Mc.292
O. micrantha Lindl.	a G bulb	I, II	BL.2025
Oreosolen wattii Hook.f. *	a H ros	IX	BL.2124, M.1095, W.230, Z.535, Sm.s.n.
Oxalis corniculata L. *	a H rept	I	Z.1842
O. corniculata var. *villosa* (Bieb.) Hohen +	a H rept	?	Onyon 9
Oxyria digyna (L.) Hill *	a G rad	VIII	By.287, M.1004, P.s.n., S.7598, Z.599, Sm.s.n.
Oxytropis arenae-ripariae Vass.	a H caesp	VIII	S.7109
O. nepalensis Vass.	a H caesp/rept	VI	BL.2107
O. williamsii Vass. *	a H caesp	IX	By.758
Paris polyphylla Smith *	a G rhiz	I	Z.449
Parnassia chinensis Franch.	a H ros	IV	M.s.n., Sm.s.n.
P. kumaonica Nekrassova	a H ros	IV, VIII	By.346, M.864, Mc.328
P. nubicola Wall. ex Royle *	a H sem	IV, VIII	By.518, L.0128, M.900
P. pusilla Wall. ex Arn.	a H ros	IV, VIII	BL.2184, H.11, Mc.352, Sm.s.n.
Parochetus communis Buch.-Ham ex D. Don *	T rept	V	By.s.n., W.423
Pedicularis bifida (Buch.-Ham. ex D. Don) Pennell	a H caesp/scap	?	By.361
P. brevifolia D. Don	a H sem	VI	P.R.294
P. clarkei Hook.f.	a G rad/H scap	V	B.5649
P. confertiflora Prain	T sem	VIII	H.29
P. elwesii Hook.f.	H caesp/G rad	VII, VIII	BL.2093, By.258, D.351, W.286
P. flexuosa Hook.f.	a H sem	III	Beer 25339
P. furfuracea Wall. ex Benth.	a H sem	III	BL.2030, Mc.268
P. gracilis Wall. ex Benth.	a H scap	V	B.5647, By.371, M.896
P. longiflora var. *tubiformis* (Klotzsch) Tsoong *	a H ros/G rad	VIII	H.31, BL.2181, By.277
P. megalantha D. Don	a H scap/G rad	III, V, VII	By.289, 641, M.846
P. microcalyx Hook.f.	G rad/scap	VII	BL.2137
P. mollis Wall. ex Benth.	a H caesp/scap	II, V	B.5697, By.247, H.1, P.55
P. muscoides L.	a H ros/G rad	VIII	BL.2129, Mc.366
P. nana C. E. C. Fischer	a H ros/sem	VI, VII	D.433
P. oederi subsp. *oederi* var. *heteroglossa* Prain *	G rad/H sem	VIII	D.411
P. pseudoregeliana Tsoong	a H ros	II, VII	BL.2086, 2201, S.4603
P. punctata Decr. +	a H caesp/scap	?	By.460
P. rhinanthoides Schrenk.	a H caesp	?	By.122
P. roylei Maxim.	a H caesp	VIII	By.440, D.382
P. scullyana Prain ex Maxim. *	a H scap	VII	By.422, Shresta 5661, Sm.s.n.
P. siphonanta D. Don	a H ros/caesp/G rad	VIII	BL.2180, By.434, D.381
P. trichoglossa Hook.f. *	a H scap	VII	By.368, D.350, L.0185, M.965, P.G.234
P. wallichii Bunge	a H sem	VII	Mc.285
Pegaeophyton minutum Hara	a H caesp/a f Ch herb pulv	VIII	BL.2088, Mc.388
P. scapiflorum (Hook.f. & Thoms.) Marq. & Shaw *	a G rhiz/a f Ch herb pulv	IX, X	M.1099, Mc.335, 373
Pentapanax leschenaultii (DC.) Seem. *	a Mi P caesp	I	BL.2158

Peracarpa carnosa (Wall.) Hook.f. & Thoms.	T rept/scap	I	Z.778
Peristylus elisabethae (Duthie) Gupta	a G bulb	V	H.60
Peristylus fallax Lindl.	a G bulb	II	Mc.396
Persicaria glacialis (Meisn.) Hara	T rept	VIII	M.917, W.244
P. microcephala var. *sphaerocephala* (Wall. ex Meisn.) Hara	a H rept	I, II	Z.737
P. polystachya (Wall. ex Meisn.) H. Gross	a G rhiz	I, II	P.s.n., Sch.2036, 2039
P. runcinata (Buch.-Ham ex D. Don) H. Gross		I, II	P.s.n.
Philadelphus tomentosus Wall. ex G. Don *	a NP caesp	I, II	L.2089, S.4630, Z.733, 1829
Phleum alpinum L.	a H caesp	X	P.G.311, W.428
Phlomis macrophylla Wall. ex Benth.	a H scap	V	By.585, P.R.310, Sch.2190, 2280, Z.776
P. rotata Benth. ex Hook.f. *	a H ros	IX	BL.2130, M.1055, P.G.242, Z.307, 578, Sm.s.n.
Phyllanthus clarkei Hook.f.	a Ch frut/a NP caesp	II, V	M.819
Physospermopsis obtusiuscula (DC.) C. Norman	a G rad	IX	M.1036
Picrorhiza scrophulariiflora Pennell	a G rhiz/ros	VII	BL.2051, Mc.280
Pieris formosa (Wall.) D. Don *	s NP scap	I, III	By.911, M.857, P.s.n., Z.1719, 1937
Pilea racemosa (Royle) Tuyama	a G bulb	III	W.333
P. symmeria Wedd.	a G rhiz	I	BL.2014
Pinguicola alpina L. *	a H ros	IV	Beer 25369, S.660
Pinus wallichiana A. B. Jackson *	b Mes P scap	II	M.s.n.
Piptanthus nepalensis (Hook.) D. Don *	a Mi P scap	II, III	By.1175, P.s.n., Sch.2082
Platanthera clavigera Lindl.	a G bulb	V	H.65
P. latilabris Lindl.	a G bulb	V	H.66, L.0171
Pleione hookeriana (Lindl.) J. Moore	fac a GE bulb	I	M.s.n. (Göttingen, Bot. Garden)
Pleurospermum angelicoides (DC.) C. B. Clarke	a G rad	V	P.s.n.
P. apiolens C. B. Clarke	a G rad	V, VII	M.910a, 937, 987, 1016, P.s.n.
P. benthamii (DC.) C. B. Clarke *	a G rad	III	By.644, L.7, M.921
P. brunonis (DC.) C. B. Clarke	a G rad	II	M.847
P. aff. *corydalifolium* Aitch. & Hemsl. +	a G rad	?	By.656
P. dentatum (DC.) C. B. Clarke	a G rad	?	By.663, 831
P. hookeri C. B. Clarke	a G rad	VIII	By.449, M.1085, Sm.s.n.
P. rotundatum C. B. Clarke	a G rad	III, V	By.663, 831, M.910b
Poa annua L.	T caesp	VII, X	Sm.s.n.
P. hirtiglumis Hook.f.	a H caesp	?	W.243
P. pagophila Bor	a H caesp	X	M.1103, Sm.s.n.
P. polycolea Stapf	a H caesp	VI, IX, X	P.G.306
Podophyllum hexandrum Royle *	a G bulb	V	Z.618
Polygonatum cf. *cirrhifolium* (Wall.) Royle *	a G rhiz	III, V	S.7124
P. hookeri Baker *	a G rhiz	VI, V	BL.2066, By.880, M.941, Sm.s.n.

P. cf. *kingianum* Colett & Hemsl. +	a G rhiz	I	P.s.n.
P. verticillatum (L.) All.	a G rhiz	III	By.878, M.926, Mc.303, Z.669
Ponerorchis chusua (D. Don) Soó *	a G bulb	III, V	By.226
Potentilla argyrophylla Wall. ex Lehm. *	a H sem	VII	D.403, S.4774
P. argyrophylla Wall. ex Lehm. var. *argyrophylla*	a H sem	VI	P.G.255, Z.586
P. argyrophylla var. *atrosanguinea* (Lodd.) Hook.f. *	a H sem	II, V	f.M.
P. caliginosa Soják	a H sem	IX	Sw.258
P. coriandrifolia D. Don *	a H sem	VI, IX	D.363, Mc.383, P.35
P. cuneata Wall. ex Lehm. *	a H rept/f Ch herb pulv	II, V, VII	By.196, D.329, M.874, P.33, 34, Sch.2035, W.439, Z.468, 613
P. eriocarpa Wall. ex Lehm. *	a G rhiz	VII, VIII, X	D.425, W.438, Sm.s.n.
P. fruticosa var. *rigida* (Wall. ex Lehm.) Wolf *	a Ch frut	VII, X	BL.2159, 2533, H.21, D.329, M.852, 1079, P.G.294, G.724, S.4752, Sch.2033, 2034, Z.613
P. fulgens Wall. ex Hook.	a H sem	II, V, VI, IX	M.821, 878, Z.1659
P. griffithii Hook.f.	a H caesp	V	P.G.338
P. cf. *kleiniana* Wight	a H sem	V	M.888
P. leschenaultiana Seringe	a H sem	V–VII	By.942, D.348
P. leuconota D. Don	a H sem	III, V	BL.2053, M.974, W.418
P. microphylla D. Don *	a f Ch herb pulv	IX	By.1097, Mc.251
P. microphylla var. *achilleifolia* Hook.f.	a f Ch herb pulv	IX	D.349, M.1038, Z.619, 665a
P. microphylla D. Don var. *microphylla*	a f Ch herb pulv	IX	M.967, 1073
P. monanthes Wall. ex Lehm.	a H sem	VI	BL.2108, Z.580a
P. peduncularis D. Don *	a H sem	VI	D.364, Z.656
P. polyphylla Wall. ex Lehm.	a H sem/G rhiz	V, VI	By.233, S.4689, 4787
P. saundersiana Royle	a H sem	V	By.45, 208, M.1025, Z.500, 628, 685, 1610a
Primula alpicola var. *luna* (Stapf) W. W. Sm. & Hetcher +	a H ros	VIII	Sch.2015
P. atrodentata W. W. Sm. *	a H ros	VIII	By.417, S.4817, Z.269, 340, 512, 563, Sm.s.n.
P. buryana Balf.f.	a H ros	III, VIII	BL.2054, Mc.378
P. calderiana subsp. *strumosa* (Balf.f. & Cooper) A. J. Richards *	a H ros	V	Beer 25354, Mc.281
P. capitata Hook.f. subsp. *capitata*	a H ros	V	Sch.2012
P. capitata subsp. *crispata* (Balf.f. & W. W. Sm.) W. W. Sm. & Forrest	a H ros	VII	Beer 25408
P. caveana W. W. Smith *	a H ros	IX	BL.2123A, P.G.283, S.6596, W.261, Z.1508, Sm.s.n.
P. concinna Watt	a H ros	VIII, IX	M.1059, 1109, Z.1505, Sm.s.n.
P. denticulata Sm. *	a H ros	I, III, V	By.129, P.s.n., Sch.2198, 2292, Z.370, 402, 505
P. deuteronana Craib	a H ros	IX	S.4530, Z.815c

P. dickieana Watt	a H ros	V, VII	Beer 25352
P. gambeliana Watt	a H ros	III, V	By.390, BL.2037, Z.815
P. geraniifolia Hook.f. *	a H ros	I, III	BL.2173, Mc.390, Z.726, 1747
P. glabra Klatt	a H ros	V	Z.814
P. glomerata Pax. *	a H ros	III, V	By.352, 649, dH.2983A, H.57, M.894, 991, Z.816, Sm.s.n.
P. gracilipes Craib	a H ros	III	S.4526
P. hookeri Watt	a H ros		Beer 25374
P. listeri King ex Hook.f.	a H ros	I	S.6975, Z.779
P. macrophylla D. Don *	a H ros	VII	BL.2097, W.278
P. macrophylla var. *moorcroftiana* (Wall. ex Klatt) W. W. Sm. & Fletcher	a H ros	VIII	Z.1463
P. megalocarpa Hara	a H ros	VIII	Beer 25373, BL.2192, dH.2986, M.984, P.G.284, Z.1565, Sm.s.n.
P. muscoides Hook.f. ex Watt	a f Ch herb pulv	VII	Mc.389
P. obliqua W. W. Sm. *	a H ros	V, VIII	Beer 25353, Mc.382
P. primulina (Spreng.) Hara *	a H ros	VI, VIII	By.442, BL.2094, D.383, 432, M.972, W.259, Z.s.n., 802, Sm.s.n.
P. pulchra Watt	a H ros	VIII	BL.2039, S.7090
P. reticulata Wall.	a H ros	VIII	Mc.406
P. rotundifolia Wall. *	a H ros	VII, VIII	By.436, D.361, M.909, Mc.278, L.0187, Z.506, 636, 1700, Sm.s.n.
P. scapigera (Hook.f.) Craib	a H ros	III	Z.800
P. sikkimensis Hook.f. *	a H ros	VIII	By.547, 592, 605, 636, 649, 1500, D.369, Sm.s.n.
P. stuartii Wall. *	a H ros	VII	Mc.386
P. tanneri subsp. *nepalensis* (W. W. Sm.) A. J. Richards	a H ros	III	Z.799
P. tenuiloba (Watt) Pax	T ros	VIII	BL.2191
P. uniflora Klatt	a H ros	VIII, IX	Beer 25360, S.1649
P. walshii Craib *	a H ros	VI, IX	P.s.n., Z.282, 511, 522, Sm.s.n.
P. wollastonii Balf.f. *	a H ros	III, IV, VIII	BL.2101, 2136, By.274, D.402, H.18, M.842, P.R.312, Z.1626, 1807, Sm.s.n.
Prunella vulgaris L.	T scap	?	By.585, W.414
Prunus rufa Hook.f. *	a Mi P scap	III	Sch.2256
Pseudostellaria heterantha (Maxim.) Pax	a G bulb	?	By.828
P. heterantha var. *himalaica* Ohwi	a G bulb	VI, VII	D.344
Pueraria peduncularis (Benth.) Grah.	a/e d PL suff	II	dH.2911A
Pyrola sikkimensis Křísa	a H sem	I	Z.483
Quercus glauca Thunb. var. *glauca* *	s Mes P scap	I	D.320
Q. lanata Sm. *	s Mes P scap	I	S.4539
Q. semecarpifolia Sm.	s Mes P scap	I, II	f.M.
Rabdosia lophanthoides var. *gerardiana* (Benth.) Hara	a H scap	II	Z.1879

Ranunculus adoxifolius Hand.-Mazz. *	a H ros	III	S.7091
R. brotherusii Freyn var. *brotherusii* *	a H ros	VII, VIII	D.338, H.38, Sm.s.n.
R. brotherusii var. *tanguticus* (Maxim.) Tamura	a H ros	VIII, IX	W.202
R. diffusus DC.	a H ros	I, II	Z.745
R. hirtellus Royle ex D. Don *	a H ros	VII, VIII	W.458, Z.582, Sm.s.n.
R. hyperboreus Rottb.	a H ros	VIII	Sm.s.n.
R. oreionannos Marq. & Shaw	a H ros	VIII	BL.2080, 2189, Sm.s.n.
R. pedatifidus Sm. +	a H sem	V	P.R.284
R. pegaeus Hand.-Mazz.	a H ros, fac hyd	VIII	BL.2146, W.197
R. pulchellus C. A. Meyer *	a H ros	VIII	By.230, BL.2076, M.1113, 1115, P.s.n.
R. pulchellus var. *ellipticus* Tamura +	a H ros	III	S.7092
R. pulchellus var. *sericeus* Hook.f. & Thoms.	a H ros	VIII	Sm.s.n.
R. pulchellus var. *stracheyanus* (Maxim.) Hand.-Mazz.	a H ros	IX	BL.2106, D.406, S.7110, Z.596
Ranunculus sp.	a H ros	?	W.305
Rheum acuminatum Hook.f. & Thoms. ex Hook.	a H sem/G rad	VII	By.653, L.0203, M.1002, S.7134
Rhodiola amabilis (H. Ohba) H. Ohba	a Ch l succ	?	By.780
R. bupleuroides (Wall. ex Hook.f. & Thoms.) Fu *	a Ch l succ/G rad	IV, IX	Beer 25514, BL.2154, By.180, M.1017, 1044, P.G.233, Sm.s.n.
R. crenulata (Hook.f. & Thoms.) H. Ohba	a Ch l succ	VIII, X	By.779, M.1063, W.168, Sm.s.n.
R. cretinii (R.-Hamet) H. Ohba	a Ch l succ/G rhiz/caesp	VIII	BL.2077
R. discolor (Franch.) Fu	a Ch l succ/caesp	IX	L.0211, Mc.349, S.4615
R. fastigiata (Hook.f. & Thoms.) Fu *	a Ch l succ/a f Ch herb pulv	IX, X	BL.2084, 2085, 2095, By.49, M.1105, Mc.339, Z.1514
R. himalensis (D. Don) Fu *	a Ch l succ	IX	By.408, D.378, Sch.2180, Z.701, Sm.s.n.
R. humilis (Hook.f. & Thoms. emend. R.-Hamet) Fu	a Ch l succ	IV	M.863
R. ovatisepala (R.-Hamet) Fu	e Ch l succ	IV	H.13, 68, M.841
R. prainii (R.-Hamet) H. Ohba	a Ch l succ	VII, VIII	D.396, 397
R. quadrifida (Pallas) Fischer & Meyer *	a Ch l succ	X	M.1062, 1096
R. sinuata (Royle ex Edgew.) Fu	a Ch l succ	III, IV	By.702, 793, 794, M.838, Mc.270, P.103, Z.1628
R. wallichiana (Hook.) Fu *	a Ch l succ	IV, VIII	H.27, 58, M.923, P.R.301, s.n.
Rhododendron anthopogon * D. Don var. *anthopogon*	s NP caesp/s Ch frut pulv	VII	M.951
R. anthopogon var. *hypenanthum* (Balf.f.) Hara	s NP caesp/s Ch frut pulv	VII	Z.562, 1552, 1812, Sm.s.n.
R. arboreum Smith *	s Mes P scap	I–III	By.30, 31, 972, M.823, Sch.2297, Z.498
R. arboreum var. *cinnamomeum* (Wall. ex G. Don) Lindl.	s Mes P scap	I–III	Mc.46, Sch.2187, Z.271, 371, 497, 1784
R. barbatum Wall. ex G. Don *	s Mi P caesp	I, III	By.554, 605, 606, S.4525, Z.1848

R. campanulatum var. *wallichii* (Hook.f.) Hook.f. *	s Mi P caesp	I, III	Mc.47, S.4527, Sch.2252
R. campylocarpum Hook.f.	s Mi P caesp	III	By.100a, s.n., M.856, 931, Mc.49, Sch.2188, S.2252, 4602, Z.373, 412, 499
R. ciliatum Hook.f. *	s NP caesp/s Ch frut	I, III	Mc.57, S.4613, Z.793
R. cinnabarinum Hook.f. *	s Mi P caesp	I	By.186, BL.2031, Mc.277, S.4532
R. dalhousiae Hook.f. *	s NP caesp/fac E	I	Z.463
R. fulgens Hook.f.	s NP caesp/s Mi P caesp	III	M.930, Mc.288, S.4524
R. hodgsonii Hook.f. *	s Mi P caesp	III	By.685, 686, 968, Mc.48, S.4521, Sch.2343, W.411, Z.645
R. lepidotum Wall. ex G. Don *	s/a NP caesp	I–III, V	By.184, 296, 385, 659, 1008, 1109, D.347, M.853, 860, Sch.2281, Z.673, 1669, 1782, 1783B
R. lepidotum var. *eleagnoides* (Hook.f.) Hook.f.	s/a NP caesp	V, VII	Sm.s.n.
R. lindleyi T. Moore *	s NP caesp/fac E	I	Mc.39, S.4531
R. nivale Hook.f. *	s Ch frut/s Ch frut pulv	VII, IX	By.915, D.430, M.996, Sch.2269, Z.523A, 538, 1484, 1811, Sm.s.n.
R. setosum D. Don *	s NP caesp/s Ch frut pulv	VII	By.688, M.950, Sch.2048, P.s.n., W.442, Z.504, 590, 1810, Sm.s.n.
R. triflorum Hook.f. *	s NP caesp/s Ch frut	I, II	Mc.40, Sch.2048, S.4520, Z.431
R. wightii Hook.f. *	s Mi P caesp	III	Z.1784A
Ribes glaciale Wall.	a NP caesp	III, V	M.920
R. griffithii Hook.f. & Thoms. *	a NP caesp	III	S.4534
R. himalense Royle ex Decne.	a NP caesp	I	Z.414, 462
R. luridum Hook.f. & Thoms.	a NP caesp	VII	D.355
R. orientale Desf. *	a NP caesp	I	Z.430
R. takare D. Don *	a NP caesp	III	S.5947
R. takare forma *desmocarpum* Hara	a NP caesp	III	S.6982
R. vilmorinii Janczew.	a NP caesp	V	Z.616
Rodgersia nepalensis T. A. Cope ex Cullen *	e G rad	II	L.0152, S.4619
Rosa macrophylla Lindl. *	a NP caesp	III, V	By.5, dH.2976, L.0168, P.37
R. sericea Lindl. *	a NP caesp	III, V	By.17, dH.2938, M.855, P.38, 39, R.278, 305
Roscoea alpina Royle *	a G rad	I–III, V	f.M., By.18, 327, 372
Rubus biflorus Buch.-Ham. ex Smith	a NP caesp	?	By.579
R. fockeanus Kurz	a Ch frut rept	V	Z.692
R. hypargyrus var. *niveus* (Wall. ex G. Don) Hara	a NP caesp/a PL frut	V	dH.2990, M.904, P.40
R. nepalensis (Hook.f.) Kuntze *	a Ch frut rept	I, II	dH.2931
R. paniculatus Smith *	a d PL frut	I, IV	dH.2931
Rumex nepalensis Spreng. *	a G rad	II, V, X	By.215, 395, P.s.n., Z.1720, Sm.s.n.
Sabia campanulata Wall. ex Roxb. *	a d PL frut	I	BL.2018, Z.481, 489

Salix calyculata Hook.f. ex Anderss. *	a Ch frut rept	VII	B.5678, BL.2134, By.550, D.387, 388, M.924, 952, Sm.s.n.
S. daltoniana Anderss.	a Ch frut/a NP caesp	III, VII	By.6, 446, D.457, M.1003, W.343, Z.376
S. disperma Roxb. ex D. Don	a Mi P scap	I	Z.471
S. eriostachya Wall. ex Anderss.	a Ch frut rept	VII	By.189, 531, W.311
S. hylematica Schneid.	a Ch frut rept	VII	By.543, D.354, 437, W.431, Z.1518
S. cf. *insignis* Anderss. +	a NP caesp	IX	P.R.344
S. lindleyana Wall. ex Anderss.	a Ch frut rept/f pulv	III, VII	D.436, M.962, 990, 1005, Sm.s.n.
S. longifora Anderss.	a Mi P scap	I	Z.387
S. luctuosa H. Lév.	a NP caesp	I, V	Z.388, 491
S. serpyllum Anderss.	a Ch frut rept	VII	Z.1518
S. sikkimensis Anderss. *	a NP caesp	VII	BL.2118, W.419
S. tetrasperma Roxb.	a NP caesp	I	Z.479
Salix sp.	a NP caesp	?	dH.2987
Salix sp.	a Mi P scap	III	M.922
Salvia campanulata Wall. ex Benth. *	a H sem	V	By.204, S.7141, Z.371A, 374, 407, 654, 1813
S. castanea Diels	a H sem	V	By.973, P.s.n., Sch.2055, 2057
S. hians Royle ex Benth. *	a H sem	V	BL.2151, By.194, D.447, M.825
Sanguisorba diandra (Hook.f.) Nordborg	a H scap	III–V	M.871, P.42
Sanicula elata Buch.-Ham. ex D. Don	a H sem	V	D.324
Sarocococca hookeriana Baill.	s NP caesp	I, II	f.M., Sch.2083
Satyrium ciliatum Lindl.	a G bulb	V	By.646, H.64
S. nepalense D. Don *	a G bulb	II, V	dH.2881, H.69, P.26
Saussurea auriculata (DC.) Sch. Bip. *	a H sem	V	By.622
S. candolleana (DC.) Sch. Bip.	a H scap	V	P.R.352
S. deltoidea (DC.) Sch. Bip. *	a H scap	I	P.s.n.
S. gnaphalodes (Royle ex DC.) Sch. Bip. *	a G rad/H ros	X	P.G.236, 256, 296
S. gossypiphora D. Don *	a H scap/G rad	X	By.145, M.1000, 1046, 1084, P.G.218, 279, W.215, Z.1452, Sm.s.n.
S. graminifolia Wall. ex DC. *	a H scap/g Ch herb pulv/G rad	X	M.1061, P.s.n., Z.1450, Sm.s.n.
S. hieracioides Hook.f.	a G rad/H ros	X	P.R.335, W.212, Z.1476, Sm.s.n.
S. leontodontoides (DC.) Sch. Bip.	a H ros/G rad/f Ch herb pulv	VI, IX, X	By.558, 1135, M.953, 995, 1081, W.226, Sm.s.n.
S. leontodontoides var. *filicifolia* (Hook.f.) Hand.-Mazz.	a H ros	IX, X	P.s.n. (f.Enum)
S. nepalensis Spreng. *	a H ros	V	P.s.n.
S. simpsoniana (Field. & Gardn.) Lipschitz *	a G rad/f Ch herb pulv/H scap	X	M.1046A, S.6583, W.214, Z.1516, Sm.s.n.
S. tridactyla Sch. Bip. ex Hook.f.	a H scap/G rad	X	M.1047, Z.576, Sm.s.n.
S. uniflora Wall. ex Sch. Bip.	a H scap/G rad	III, V	Beer 25390
S. wernerioides Sch. Bip. ex Hook.f.	a f Ch herb pulv	IX, X	M.1049, P.G.235, W.217, Sm.s.n.
S. yakla C. B. Clarke	H ros/G rad	IX, X	P.R.303, W.385
Saussurea sp.	a G rad/ros	III, IV	M.919
Saxifraga andersonii Engl. *	e g Ch herb pulv	IX	D.419, 443, Z.566, Sm.s.n.

S. *aristulata* Hook.f. & Thoms.	g H herb pulv	IV, VI	By.673, H.27, 52, M.843, 907, P.G.214, W.211, Z.1479, 1526, 1615B, Sm.s.n.
S. *brachypoda* D. Don *	e H scap	IV	Beer 25412, By.489, 666, H.7, M.843, Sm.s.n., P.s.n., W.287, Z.1876
S. *brunonis* Wall. ex Seringe *	e H ros	VI, IX	By.487, M.1018, P.R.350, W.338, Sm.s.n.
S. *cordigera* Hook.f. & Thoms.	H sem	IV, IX, X	Beer 10003
S. *diversifolia* Wall. ex Seringe	a H sem	V	P.48, Z.1292, 1805
S. *engleriana* H. Smith *	e H ros	X	Mc.332, S.7106, Sm.s.n.
S. *filicaulis* Wall. ex Seringe	e H caesp/scap/f Ch herb pulv	IV, VII	By.604, M.865, Z.s.n.
S. *gageana* W. W. Smith	e H ros	IV, VII, IX	Beer 9581, M.1020
S. *georgei* Anthony	e g Ch herb pulv	X	Sw.500
S. *granulifera* H. Smith	a H ros	III, V	dH.2975, M.898, P.R.340, W.284, Z.1506, Sm.s.n.
S. *hirculoides* Decne.	a H ros/f Ch herb pulv	IX, X	By.542, P.G.s.n., Sm.s.n.
S. *hispidula* D. Don	a H caesp	IV, VI, IX	M.908, 1020, P.G.331, W.260
S. *hookeri* Engl. & Irmsch.	a H ros	X	P.47, S.628, W.374
S. *jacquemontiana* Decne. *	e H ros/g Ch herb pulv	IX, X	M.1086
S. *lowndesii* H. Smith	e H ros/rept/g Ch herb pulv/G rhiz	X	Sw.421
S. *lychnitis* Hook.f. & Thoms. *	a f Ch herb pulv	VIII–X	M.1089, Mc.329, Sm.s.n.
S. cf. *melanocentra* Franch. *	a H ros	X	By.450, Sm.s.n.
S. *moorcroftiana* (Seringe) Wall. ex Sternb.	a g Ch herb pulv/H ros	VI	M.1026, Z.1549
S. *mucronulata* Royle *	e H ros	X	By.443, D.417, M.1013, Z.1615a, Sm.s.n.
S. *mucronulata* subsp. *sikkimensis* (Hulten) Hara	e H ros/rept	X	BL.2115, Mc.356
S. *nutans* Hook.f. & Thoms.	a H ros/Ch herb pulv	IX	H.30, W.207, 287, Z.1526, 1623, Sm.s.n.
S. *pallida* Wall. ex Seringe	a H sem	III, IV	BL.2156, By.515, D.352, 440, L.2202, Mc.297, S.4780
S. *palpebrata* Hook.f. & Thoms.	a H sem	III, IV	Beer 9554, D.461
S. *parnassifolia* D. Don *	a H sem	IV	By.391, 781, M.810, Z.1805
S. *perpusilla* Hook.f. & Thoms.	e H ros/f Ch herb pulv	X	M.1064, 1106, Mc.340, P.G.237, W.232
S. *pilifera* Hook.f. & Thoms.	e H ros/rept	VIII	BL.2143, Sm.s.n.
S. *pseudo-pallida* Engl. & Irmsch. *	a H ros	VIII, IX	BL.2095, D.398, 438, M.1012, Mc.333, Sm.s.n.
S. *punctulata* Engl.	e H ros	X	BL.2145, M.1078, P.G.274, W.180, Sm.s.n.
S. *roylei* H. Sm. *	e f Ch herb pulv	IV, IX	P.s.n.
S. *saginoides* Hook.f. & Thoms. *	e g Ch herb pulv	IX, X	BL.2141, By.778, D.413, H.42, M.1040a, Mc.331, P.G.238, W.161, 223, 277, Sm.s.n.
S. *serrula* H. Smith	e H rept/caesp	IV, V	P.50
S. *sibirica* L. *	a H ros/sem	IV	B.5777, By.512
S. *sikkimensis* Engl.	a H scap	III, IV	Beer 25512, S.1644

S. stella-aurea Hook.f. & Thoms.	e H ros/rept/f Ch herb pulv	X	BL.2145, M.1100, Sm.s.n.
S. stenophylla subsp. *hoffmeisteri* (Klotzsch) Hara *	e H ros/rept	X	M.1118
S. strigosa Wall. ex Seringe *	a H sem/rept	IV	By.660, M.906, P.51, Z.1660
Schisandra grandiflora (Wall.) Hook.f. & Thoms. *	a d PL frut	I	Z.716
Scopolia stramonifolia (Wall.) Shrestha *	a H scap	V	f.M.
Scrophularia pauciflora Benth.	a G rhiz/scap	III	B.5679
Sedum chauveaudii R.-Hamet	a Ch l succ	IV	Z.1679
S. gagei R.-Hamet	a H scap	IV	H.22, M.1020, Z.1609
S. oreades (Decne.) R.-Hamet *	a Ch l succ	VI, IX	By. 620
S. triactina Berger	a Ch l succ/caesp	I, IV	Mc.270
S. trullipetalum Hook.f. & Thoms.	a Ch l succ	IV	M.862, 960, W.273, 301
Selinum candollii DC.	a G rad	?	By.13, 245, 655
S. cortioides C. Norman	a G rad	VI, IX	M.1001a
S. tenuifolium Wall. ex C. B. Clarke *	a G rad	V	M.848, 883a
Senecio alatus Wall. ex DC.	a H sem	I, II	Z.1634, 1770
S. albopurpureus Kitam.	a H ros	VIII, X	M.1052
S. cappa Buch.-Ham. ex D. Don	a Ch suff	II	Z.1740A, 1845
S. chrysanthemoides DC. *	a H sem/scap	II, V	By.197, 399
S. diversifolius Wall. ex DC.	a H scap	II, V	M.827, P.s.n.
S. graciliflorus DC. *	a G rad/scap	II, V	Z.1760
S. lancifera J. R. Drummond	a H sem	V	M.829
S. rufinervis DC.	a H sem	?	P.s.n.
S. scandens Buch.-Ham. ex D. Don *	a Ch suff/L	II	dH.2909, Sch.2363, W.383, Z.1740
S. triligulatus Buch.-Ham. ex D. Don	a Ch suff	II	dH.2901, S.4487
S. wallichii DC.	a H sem	III, V	Z.1662
Sibbaldia cuneata Hornem. ex Kuntze *	a g Ch herb pulv/G rhiz	V	Z.658, 695
S. micropetala (D. Don) Hand.-Mazz.	a H sem	V	BL.2171, D.346, Z.789
S. perpusilloides (W. W. Smith) Hand.-Mazz.	a G rhiz/f Ch herb pulv	VII, X	Mc.379
S. purpurea Royle *	a G rhiz/f Ch herb pulv	IX, X	M.1039, 1077, Mc.377, Z.568, Sm.s.n.
Silene aff. *gonosperma* (Rupr.) Bocquet	a H caesp	VII	M.1027
S. gonosperma subsp. *himalayensis* (Rohrb.) Bocquet var. *himalayensis*	a H caesp	IX	BL.2187, By.432, Sm.s.n.
S. nigrescens (Edgew.) Majumdar	a G rhiz/H sem	VI, VII	M.1006, Sm.s.n.
S. setisperma Majumdar	a H scap	?	Sm.s.n.
S. thomsonii Majumdar	a H sem	III, IV	M.968, P.s.n.
Sinocarum sp.	a G rad	VI	M.s.n.
Skimmia laureola (DC.) Sieb. & Zucc. ex Walp. *	s NP caesp	I	S.2064, 4477
Smilacina oleracea (Baker) Hook.f. *	a G rhiz	II	Mc.267, S.4627
S. purpurea Wall. *	a G rhiz	II, III	Mc.291
Smilax menispermoidea DC.	s d PL frut	I	Mc.55, 423, 1783
Sorbus cuspidata (Spach) Hedlund *	a Mes P scap	III	M.824

S. foliolosa (Wall.) Spach	a Mi P scap	III	M.893
S. hedlundii Schneid.	a Mi P scap	I	P.s.n.
S. microphylla Wenzig *	a Mi P scap	III	By.7, 839, 1155, D.451, S.6580, 7143, 7147
S. ursina (Wenzig) Decne.	a Mi P scap	III	Mc.276
Soroseris hookeriana (C. B. Clarke) Stebb. *	a H ros	X	M.998, W.254
S. hookeriana (C. B. Clarke) Stebb. subsp. *hookeriana*	a H ros	X	P.G.247, Sm.s.n.
S. pumila Stebb.	a H ros	X	By.382, P.G.217, Sm.s.n.
Spathoglottis ixioides (D. Don) Lindl. *	obl. a E Ch succ	IV	By.366, M.806, L.016
Spiraea arcuata Hook.f. *	a NP caesp	III, V	By.439, M.933, P.s.n., Sm.s.n.
S. bella Sims	a NP caesp	II	S.4628
S. canescens D. Don *	a NP caesp	II	S.7122
Spiranthes sinensis (Pers.) Ames *	a G rad	V	H.62–64, M.835
Stellaria congestiflora Hara	a H rept	VIII, X	W.246
S. decumbens Edgew. *	e H rept/e f Ch herb pulv	X	M.1022, Sm.s.n.
S. decumbens var. *polyantha* Edgew. & Hook.f.	a H rept	X	BL.2028, By.387, M.971
S. decumbens var. *pulvinata* Edgew. & Hook.f.	a f Ch herb pulv/a H rept	VIII, X	M.s.n.
S. graminea L.	a H rept	IV, VIII	M.897
S. lanata Hook.f. ex Edgew. & Hook.f.	a H rept	?	W.373
S. sikkimensis Hook.f. ex Edgew. & Hook.f.	T rept	?	W.380
Streptopus simplex D. Don *	a G rad	III	By.138, BL.2017, L.0158, Z.777
Sunipia bicolor Lindl.	obl. e E Ch succ	I	Sch.2312
Swertia cuneata D. Don	a H sem	VII, VIII	M.949, 1057, P.160, R.328
S. dilatata C. B. Clarke	a H scap	V	M.918
S. hookeri C. B. Clarke *	a H sem/G rad	VII	S.7087
S. kingii Hook.f.	a H sem/G rad	V	L.0419, W.290
S. multicaulis D. Don	a G rad/H caesp	VII	By.504, 524, D.339, H.44, P.G.209, G.285, W.234, Sm.s.n.
Sympagis petiolaris (Nees) Bremek.		II	Z.1743
Symplocos paniculata (Thunb.) Miq. *	s/a Mi P scap/caesp	I	S.4623
S. sumuntia Buch.-Ham. ex D. Don	s Mi P scap	I	S.4483
Tanacetum atkinsonii (C. B. Clarke) Kitam. *	a H sem	V, VI	P.s.n.
T. gossypinum Hook.f. & Thoms. ex C. B. Clarke *	a H ros/scap	IX, X	By.1176, H.39, Sm.s.n., M.1031, 1070, P.G.211, G.295, Sch.2315, W.179, Z.1509
Taraxacum mitalii van Soest	a G rad/H ros	V–VII	Z.270
T. monochlamydeum Hand.-Mazz.	a G rad/H ros	V	Z.1763
T. pseudostenoceras van Soest	a G rad/H ros	V, VI	Z.1603
Taxus baccata subsp. *wallichiana* (Zucc.) Pilger	b N/Mi P scap	I	f.M., Sch.2056, 2939, S.4496

Thalictrum alpinum L. *	a H ros	VI, VII, IX	D.394, 400, BL.2111, Z.644, Sm.s.n.
T. cultratum Wall. *	a H sem	V	S.7140, Sm.s.n.
T. elegans Wall. ex Royle	a H sem	V	P.s.n., W.405
T. reniforme Wall. *	a H sem	V	By.176, 191, M.890, S.7146
T. virgatum Hook.f. & Thoms. *	a H sem	I, II	BL.2169, D.323, P.s.n., Sch.2099
Thermopsis barbata Royle *	a G rad	V	By.511, 552, 949, dH.2956, Sch.2053, 2054, 2174, Z.1646
Thesium himalense Royle ex Edgew.	a G rad	V, VII	P.42, Z.501, 682
Tiarella polyphylla D. Don	a H sem	I, II	P.53, Z.448, 768
Tofieldia himalaica Baker	a G rhiz	VI, VII	M.964
Trachydium aff. *roylei* Lindl. +	a G rad	?	By.561
Trigonotis multicaulis (DC.) Benth. ex C. B. Clarke	a H caesp	III, IV	Beer 10016, S.653
T. ovalifolia (Wall.) Benth, ex C. B. Clarke	a H scap	III	Mc.357, S.7088
T. rotundifolia (Wall. ex Benth.) Benth. ex C. B. Clarke *	a H caesp	V, VII	BL.2204, S.652
Triosteum himalayanum Wall.	a H scap	I, III, V	L.0654, P.s.n., Z.679
Triplostegia glandulifera Wall. ex DC.	a G rad	?	H.12, W.364
Tripogon filiformis Nees ex Steudel	a H caesp	IV	M.808, 817c
Tripterospermum volubile (D. Don) Hara	a el HL	I, II	Sch.2068
Trisetum scitulum Bor	a H caesp	VI, VII	P.G.303
T. spicatum (L.) K. Richter	a H caesp	VI	By.1071, M.1021a, P.R.349
Trollius pumilus D. Don	a H ros	VIII	BL.2080
Tsuga dumosa (D. Don) Eichler *	b Mes P scap	I	f.M., Sch.2340, 2360
Typhonium diversifolium Wall. ex Schott *		I	By.225
Urtica dioica L.	a G rhiz	V	f.M.
Utricularia striatula Sm.	a hyd H rept	IV	P.267
Vaccinium dunalianum Wight	s E Ch frut	I	BL.2021
V. glauco-album Hook.f. ex C. B. Clarke	s NP caesp	I	Sch.2163
V. nummularia Hook.f. & Thoms. ex C. B. Clarke *	s fac E Ch frut rept	I	S.4605, Z.266, 382
V. retusum (Griff.) Hook.f. ex C. B. Clarke	fac E/s NP caesp/Ch frut	I	P.B.75, S.4475
Valeriana hardwickii Wall.	a H scap	II	By.320, D.358, Sch.2077, Z.1672
V. jatamansii Jones *	a H sem	II	Z.263
V. stracheyi C. B. Clarke	a H scap	II	Z.1317
Verbascum thapsus L.	a H sem	V	By.182, Sch.2061, P.56, 57
Veronica cana Wall. ex Benth.	a H scap	I	P.260
V. cephaloides Pennell	a H scap	?	W.191
V. lanuginosa Benth. ex Hook.f. *	a H rept/G rhiz	X	BL.2176, M.1079, Mc.375, Sw.88–99
V. himalensis D. Don	a H scap	?	By.130
V. umbelliformis Pennell	a H scap	?	W.308
Viburnum erubescens Wall. ex DC. *	a Mi P caesp	I, II	Z.734
V. grandiflorum Wall. ex DC. *	a NP caesp	III	Z.405

V. nervosum D. Don *	a Mi P caesp	III	Mc.35, S.4523, Z.795
Vincetoxicum hirundinaria subsp. *glaucum* (Wall. ex Wight) Hara *	a G rad/scap	V	Sch.2249, Z.675, 714
Viola biflora L. *	a H ros	II, III, V	By.110, W.366, Z.579, 652, 702, 1774, Sm.s.n.
V. pilosa Blume	a H ros	I, III	Onyon 10, S.4479, Z.397
V. thomsonii Oudemans	a H ros	I	S.4486
Waldheimia glabra (Decne.) Regel *	a H ros/G rhiz	VIII, X	By.448, H.36, dH.2999, M.973, Mc.315, P.R.345, W.174, 181, Z.1453, Sm.s.n.
Youngia japonica (L.) DC.	a H sem	I, II	Z.748
Y. racemifera (Hook.f.) Babcock & Stebb.	a H sem/a G rad	III	M.976, W.319
Ypsilandra yunnanensis W. W. Smith & Jeffrey	a G rad	V, VII	Beer 25356
Zanthoxylum nepalense Babu *	a/s NP caesp	II	Z.758
Z. oxyphyllum Edgew. *	a d PL frut/NP caesp	II	BL.2015, Z.465, 1695, 1866

Alphabetical list of ferns and fern allies

Adiantum pedatum L.	e rhiz	III, V	Z.1688, 1779
Anogramma leptophylla (L.) Link	a caesp	I	Z.1754
Araiostegia pulchra (Don) Copel.	a rhiz	II	Z.674
Arthromeris himalayensis (Hook.) Ching	a rhiz	I	dH.2888, Z.256
A. wallichiana (Sprengel) Ching	a rhiz	I	Z.1871
Asplenium ensiforme Wall. ex Hook. & Grev.	e caesp	I, II	Z.1896
A. varians Wall.	a caesp	III	W.357
Athyrium drepanopterum (Kunze) A. Br.	a/e caesp	I	Z.1019
A. duthiei (Bedd.) Bedd.	a rhiz	III	Z.646
A. fimbriatum (Wall.) T. Moore	a/e caesp	I	Z.1870
A. mackinnoni (Hope) Christensen	a caesp	I, III	Z.1682
A. pectinatum (Wall. ex Mett.) Bedd.	a rhiz	I, III	Z.1665
A. schimperi Moug. ex Fée	a rhiz	I	Z.678, 1752
A. schizochlamys Ching	a caesp	V	M.885A, 912A, 927
A. spinulosum (Maxim.) Milde	a rhiz	III	Z.677, 1685, 1794
Cheilanthes albomarginata C. B. Clarke	a caesp	I	Z.761
C. farinosa (Forsk.) Kaulf.	a caesp	?	W.354
C. subvillosa Hook.	a caesp	V	Z.1823
Coniogramme affinis Hieron.	e rhiz	IV	Z.725
C. caudata (Wall. ex Ettingsh.) Ching	e rhiz	IV	Z.454
C. intermedia Hieron.	e rhiz	IV	Z.1749
Crypsinus erythrocarpus (Mett. ex Kuhn) Tagawa	e rhiz	I, III	Z.1689B

Cryptogramma brunoniana Wall. ex Hook. & Grev.	a caesp	III, V, VII	M.986, W.256, Z.1562
Cystopteris dickieana Sim	e caesp	VII	M.1010A, Z.1618
C. filix-fragilis (L.) Bernh.	a caesp	V	Z.639, Sm.s.n.
Drynaria mollis Bedd.	a rhiz	I, IV, V	Z.1639
Dryopteris acuto-dentata Ching	a caesp	V	M.885B, 961
D. barbigera (T. Moore ex Hook.) Kuntze subsp. *barbigera*	a caesp	VI	M.886
D. chrysocoma (Christ) C. Chr.	a caesp	VI	Z.1642, 1684
D. fibrillosa (C. B. Clarke) Hand.-Mazz.	a caesp	III, VI	Z.1681, 1776
D. marginata (Wall. ex C. B. Clarke) Christ	a caesp	I, III, IV	Z.273
D. serratodentata (Bedd.) Hayata	a caesp	VII	M.1010B, Z.1542, 1567
D. sublacera Christ	a caesp	I	Z.385, 488
D. wallichiana (Spreng.) N. Hylander	e caesp	I, III	Z.455, 1832
Equisetum diffusum D. Don	a G rhiz	I, III	W.430
Gymnocarpium oyamense (Bak.) Ching	a rhiz	I	Z.719
Lepisorus clathratus (C. B. Clarke) Ching	e/a rhiz	III	Z.507, 638
L. contortus (Christ) Ching	e rhiz	III	Z.377, 396
L. kashyapii (Mehra) Mehra	e rhiz	I	Z.721
L. loriformis (Wall.) Ching	e rhiz	III	Z.791B
L. variabilis Ching & S. K. Wu	e/a rhiz	III	W.345
Leucostegia delavayi (Bedd.) Ching ex Christensen	a rhiz	V	Z.1625
Lycopodium clavatum L.	b Ch herb rept	I	W.387, Z.427, 1890
L. veitchii Christ	b Ch herb rept	?	W.352
Mecodium polyanthos (Sw.) Copel.	a rhiz	I, III, V	Z.703, 1895
Notholaena marantae (L.) Desv.	a caesp	I, III–V	dH.2965, M.840, 885c, 925, Z.265, 629, 1650, 1713
Oleandra wallichii (Hook.) C. Presl	e rhiz	IV	Z.754
Onychuum contiguum Hope	a rhiz	II, V	dH.2882, Z.1658
Osmunda claytonia var. *vestita* (Wall.) Milde.	e caesp	II	Z.715
Phymatodes crenatopinnata (C. B. Clarke) Ching	e rhiz	I, III	Z.1689B (*Candollea* **15:** 206 [1956])
P. ebenipes (Hook.) Ching	e rhiz	III	Z.715B, 1689
P. malacodon (Hook.) Ching	e rhiz	III, VII	W.298, Z.637, 1334, 1624
P. stewartii (Bedd.) Ching	e rhiz	I	Z.738
Plagiogyria communis Ching	e caesp	IV	Z.257, 460
Polypodium amoenum Wall. ex Mett.	e/a rhiz	I, III, IV	Z.753
P. microrhizoma C. B. Clarke ex Baker	e rhiz	V	M.912B

Polystichum acanthophyllum (Franchet) Christ	e caesp	I, III	Z.384
P. discretum (Don) Diels	a caesp	I	Z.455
P. lachenense (Hook.) Bedd.	e caesp	VI–X	M.1010c, Z.1449, 1595
P. mehrae Fraser-Jenkins & Khullar	e caesp	II	N.9
P. neolobatum Nakai	e caesp	I	Z.1680
P. nepalense (Spreng.) C. Chr.	a caesp	I, III, IV	Z.1742
P. shensoense Christ	a caesp	III	M.975
P. stimulans C. Presl	e caesp	IV	Z.1666, 1737
P. thomsonii (Hook.f.) Bedd.	a caesp	IV	W.356, Z.399, 747, 826b, 1736
Pteridium aquilinum (L.) Kuhn	a rhiz	II, III, V	M.s.n.
Pteris cretica L.	e rhiz	I	Z.1738, 1847
P. dactylina Hook.	e rhiz	I	Z.267, 487, 1737
P. subquinata Wall. ex Hope	e caesp	IV	Z.1826
P. wallichiana J. Agardh	e caesp	IV	Z.1873
Selaginella chrysocaulos (Hook.f. & Grev.) Spring		I	Z.1735
Thelypteris levingei (C. B. Clarke) Ching	a rhiz	III	Z.1686
Tricholepidium normale (D. Don) Ching	e rhiz	IV	Z.1750
Vittaria flexuosa Fée	e rhiz	IV	Z.1748
Woodsia andersonii (Bedd.) Christ	a caesp	?	W.355
W. elongata Hook.	a caesp	IV	Z.680, 1751, 1775, 1809
W. lanosa Hook.	a caesp	?	W.358

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Further genera of the Biddulphiaceae (diatoms) with interlocking linking spines

Robert Ross & Patricia A. Sims

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Further genera of the Biddulphiaceae (diatoms) with interlocking linking spines

Robert Ross and **Patricia A. Sims**
Department of Botany, British Museum (Natural History), Cromwell Road, London
SW7 5BD

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Synopsis

Descriptions are given of a number of genera of the Biddulphiales, all except one with interlocking linking spines. *Solium* Heiberg, a monotypic genus, is distinguished from *Trinacria*. *Pseudorutilaria* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni is close to *Solium* but has some unique characteristics. Five new species from the Eocene of the southern oceans are described. *Monile* R. Ross & P. A. Sims, a monotypic genus from the Miocene of southern France with similarities to both *Pseudorutilaria* and *Biddulphia*, is described as new. A new genus, *Maluina* R. Ross & P. A. Sims, is proposed for *Hemiaulus centralitenuis* R. Ross & P. A. Sims, and another monotypic new genus, *Bonea* R. Ross & P. A. Sims, is established for a tripolar diatom from the Eocene of the U.S.S.R. close to *Strelnikovia* R. Ross & P. A. Sims. New information about *Dextradonator eximius* (Grunow) R. Ross & P. A. Sims is presented. The position of genera within the family Biddulphiaceae is discussed but presents some difficulties, especially because of possible parallel evolution. The limits of the order Biddulphiales are also considered.

Introduction

In a recent paper (Ross & Sims, 1985) we dealt with a group of related genera in the diatom family Biddulphiaceae characterized by the possession of interlocking linking spines and well developed pseudocelli. In the course of preparing this we examined all the other members of the family with interlocking linking spines but concluded that none of these were close to the group with which we were dealing there. They belonged to four genera and our studies of these with the scanning electron microscope produced new information recorded here. One of these genera is *Solium* Heiberg (1863), for our examination of *S. exsculptum* Heiberg, its type species, showed that it should not be placed in *Trinacria* Heiberg (1863), the genus to which it was transferred by Hustedt (1930). Another is *Pseudorutilaria* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni (1894), of which we found five undescribed species in Eocene material from the

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Falkland Plateau in the South Atlantic. This genus is apparently close to *Solium*, but it has remarkable structural features on its central portion that clearly distinguish it. We re-examined the diatom that we earlier described as *Hemiaulus centralitenuis* R. Ross & P. A. Sims (in Ross, Sims & Hasle, 1977) and concluded that it could not be retained in *Hemiaulus* Heiberg (nom. cons. prop., see Ross, 1985), but that it was necessary to establish for it a new genus, which we have called *Maluina*. The fourth genus with interlocking linking spines is *Dextradonator* R. Ross & P. A. Sims (1980), and we present here additional information about *D. eximius* R. Ross & P. A. Sims.

We also describe here another new genus, *Bonea*, based on a single new species with interlocking linking spines. This, which comes from the Eocene of the U.S.S.R., has many similarities with the genera we described in our previous paper, especially *Strelnikovia* R. Ross & P. A. Sims (1985), but it had not come to our notice at the time when that paper was prepared. Another new genus described here, *Monile*, is also based on a single new species, one that comes from the Miocene of southern France. It does not have interlocking linking spines, but it is included here because, although there is little to separate it from *Biddulphia* Gray (1821), it has many features in common with *Pseudorutilaria*, as well as some in which it resembles *Keratophora* Pantocsek (1889) and *Strelnikovia* R. Ross & P. A. Sims. Its affinities are puzzling.

Sources of specimens and records

In the distribution lists for the species considered in this paper there are many records taken from literature, and all the information available about these is to be found in the references given. We have endeavoured to give a complete account of the known distribution of the species dealt with, but we realize that our coverage of Russian literature is incomplete, although probably sufficient to give a reasonably adequate picture. Many of the specimens that we have ourselves examined come from localities of which we gave details in our recent paper (Ross & Sims, 1985). The additional localities from which we have seen specimens are discussed below.

U.S.S.R.

Northern Urals

One of the samples that the British Museum (Natural History) received from Mr Brigger was labelled 'N. Urals, U.S.S.R., Oligocene'. We have no further information about this material but presume that it is from one of the samples that are the basis of the records from the lower Oligocene of the northern and central Urals in *Diatomovyi Analiz* (Proshkina-Lavrenko et al., 1949*a*).

Germany

Greifswalder Oie, Rostock

This is one of the localities from which Schulz (1927) reported lower Eocene diatoms. The specimen from this locality that we have seen was mounted by Hustedt and came from Schulz's sample.

Denmark

All the specimens from Denmark that we have examined come from the Moler formation of lower Eocene (Ypresian) age. The precision with which the locality is indicated varies; the specimens are said to come from: Jutland, Glyngøre, Skive, Limfjord, Island of Mors, Nykjobing, Ejerslev, Island of Fur.

France

Saint Laurent-la Vernède, Gard

The Miocene deposit from this locality is described by Lefébure (1935). We are not aware of any more precise information about its geological age.

Barbados

We have examined specimens from two localities in Barbados additional to those from which we reported specimens in our previous paper (Ross & Sims, 1985). These are Bissex Hill and Malvern Hill. No information about the level of these samples within the Oceanic Beds, which range from middle Eocene to lower Miocene, is available to us.

'Lamont E 8'

This is the only label on one sample received from Mr Brigger. Neither the California Academy of Sciences nor the Lamont-Doherty Geological Observatory have any record giving locality data for this. Its content suggests very strongly that it comes from the middle to upper Eocene of the Falkland Plateau area. Mr Brigger received a number of such samples from the Lamont-Doherty Geological Observatory and it is presumably one of these.

Terminology

The terminology used in the descriptions of the genera and species is that proposed by Ross et al. (1979), supplemented by terms that we adopted in our most recent paper (Ross & Sims, 1985: 285) and one proposed by von Stosch & Simonsen (1984: 11), viz. 'interstrial pores'. In addition we use here two new terms, 'subocellus' and 'pseudo-antiligula'.

In *Solium* Heiberg, *Pseudorutilaria* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni, and *Monile* R. Ross & P. A. Sims there is a cluster of perforations through the valve on the distal side of the upper parts of the elevations; in *Monile* this also extends onto the summit of the elevations (Fig. 64). Vela are present in these in *Solium* (Fig. 5) and *Pseudorutilaria* (Fig. 42), and probably also in *Monile*. There is, however, no transition between the small areolae in these clusters and the areolae on the rest of the valve, and in this they differ from the pseudocelli of such genera as *Biddulphia* S. F. Gray (Ross & Sims, 1971: pl. 1 fig. 2), *Briggera* R. Ross & P. A. Sims (1985: pl. 5 fig. 6), and *Trigonium* Cleve (Ross & Sims, 1971: pl. 2 fig. 6). On the other hand there is no thickened ring of silica around these clusters of small areolae such as surrounds the ocelli of *Amphitetras* Ehrenberg (Ross & Sims, 1971: pl. 5 fig. 2) and the other genera included in the Eupodiscaceae and the ocelluli of the Cymatosiraceae (Hasle et al., 1983). For these clusters of small areolae with a definite but unthickened margin we use the term 'subocellus'. We have also used this term for the small cluster of more tightly and uniformly packed perforations on the distal side of the tip of the elevations in *Maluina* R. Ross & P. A. Sims (Fig. 68) as this cluster also has no thickened rim; it may well be, however, that this cluster consists of porelli, not areolae.

In *Maluina centralitenuis* (R. Ross & P. A. Sims) R. Ross & P. A. Sims there is at each pole of the valve a downward projection of the mantle, i.e. one parallel to the pervalvar axis. Similar projections are present on the girdle bands of many species and are termed 'antiligulae'. This term cannot, however, be used for structures that are part of the valve; hence we use for them the term 'pseudo-antiligula'.

Taxonomic account

I. ***SOLIUM*** Heiberg, *Consp. crit. Diat. Dan.*: 52 (1863).

Hemiaulus subgen. *Solium* (Heiberg) Van Heurck, *Treat. Diat.*, transl. Baxter: 455 (1896).

Frustules united in short, straight, inseparable chains, the pervalvar axis from about half to about twice as long as the diameter of the valve. Valves multipolar, with short projections at each pole cut off from the central portion by transverse sulci or internal costae. Elevations at each pole moderately stout, not expanded above, with a subocellus on the distal side near the tip, linking spines on the proximal side of the tip expanded above and interlocking, except those of the end cells of chains. A well developed marginal ridge between the elevations. Mantle with the upper part areolate and with anastomosing external costae that continue onto the elevations, the lower part hyaline and deeply concave. Areolae irregularly scattered on the central portion of the valve, decussate or irregularly scattered on the projections, each occluded by a vola.

Scattered hollow spines or occluded processes sometimes present on the central portion of the valve. One labiate process on the central portion of the valve near the base of a projection, its internal opening sessile and straight, its external part tubular.

TYPE SPECIES: *Solium exsculptum* Heiberg (loc. cit.)

Heiberg (1863) established the genera *Trinacria* and *Solium* for tripolar and quadripolar diatoms with the frustules united in chains by elevations with linking spines. Bipolar diatoms forming similar colonies he placed in *Hemiaulus*. *Hemiaulus* Ehrenberg (1844) has been shown to be a later synonym of *Eucampia* Ehrenberg (1839), and the conservation of *Hemiaulus* in the sense in which Heiberg and all subsequent authors have used it has recently been proposed (Ross, 1985). H. L. Smith (1872) did not consider that the number of poles was a sufficient basis for distinguishing genera, and he regarded *Trinacria* and *Solium* as synonyms of *Hemiaulus*, as did Van Heurck (1896), who treated *Trinacria* and *Solium* as subgenera of *Hemiaulus*, and Schütt (1896), who was the only one of these authors to publish any new combinations under *Hemiaulus*. Most authors, however, maintained the three genera as separate until Hustedt (1930) united *Trinacria* and *Solium* under the name *Trinacria*, a genus he regarded as separate from *Hemiaulus*.

We would agree with the view that the number of poles is not by itself a sufficient basis for generic separation, and we are not here concerned with the question of whether or not there are other differences on which to base a separation of *Trinacria* from *Hemiaulus*. The differences, however, between *Solium exsculptum* Heiberg and *Trinacria regina* Heiberg, the type species of the two genera, are such as to justify placing them in separate genera. In *Trinacria regina* the linking spines are never expanded above and interlocking, there is no subocellus but only a poorly developed pseudocellus, the mantle is vertical throughout, and the areolae are occluded by cribra; in *Solium exsculptum* the linking spines are normally expanded above and interlocking, there is a well developed subocellus, the lower part of the mantle is strongly concave, and the areolae are occluded by volae. We attach particular importance to the presence and nature of the subocellus and the concavity of the lower part of the mantle as features separating *Solium* from *Trinacria* because they suggest, as we argue below (p. 291), that *Solium* may be more closely related to such members of the Eupodiscaceae as *Eupodiscus* J. W. Bailey (1851), *Triceratium* Ehrenb. (1839) sensu stricto, and *Amphitetras* Ehrenb. (1840), than to *Biddulphia* Gray (1821) or *Hemiaulus* Heiberg (1863). *Trinacria*, on the other hand, is much closer to *Hemiaulus* Heiberg and the majority of genera of the Biddulphiaceae.

The genus to which *Solium* is most closely related is *Pseudorutilaria* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni and we discuss their resemblances and differences after our description of that genus.

Solium exsculptum Heiberg is the only known species of the genus. The two others that have been referred to it, *S. jeremiae* (Truan & Witt) De Toni (1894) and *S. princeps* M. Peragallo (in Tempère & Peragallo, 1912) are both quadripolar species of *Trinacria*. *S. jeremiae* was originally described as *Trinacria jeremiae* Truan & Witt (1888), but *S. princeps* cannot be called *Trinacria princeps* as that name is pre-occupied. It has, however, been described independently as a new species, *Trinacria cristata* Gombos (1982).

1. **Solium exsculptum** Heiberg, *Consp. crit. Diat. Dan.*: 52 (1863).
(Pl. 1, Pl. 12 figs 86–88)

Hemiaulus exsculptus (Heiberg) Schütt in Engler & Prantl, *Naturl. Pflanzenfam.* **1** (1b): 97 (1896).
Trinacria exsculpta (Heiberg) Hustedt in Rabenhorst, *Krypt.-Fl. Deutschl., Österr. u. d. Schweiz* **7** (1): 889 (1930).

Valves with 4 or 5 projections separated from the central portion by deep sulci; length of side in 4-polar specimens 30–110 μm, maximum diameter of 5-polar specimens 35–45 μm, height at centre of valve 7·5–16 μm; central portion with straight sides between the projections, weakly domed; projections semi-circular to narrowly triangular with obtuse apices, slightly domed and rising towards the elevations. Elevations arising at the apices, not expanded above; height to their tops 18–38 μm. Areolae poroid, 0·3–0·7 μm in diameter, occluded by volae, with a raised external rim from which one or two very short cylindrical spines sometimes arise, irregularly scattered and 5–6 in 10 μm on the central portion of the valve, the projections, the elevations, and the upper part of the mantle, or decussate and rather closer, 7–8 in 10 μm, on the projections. Sparse scattered hollow spines or occluded processes sometimes present on the central portion of the valve of end cells. Subocelli on the upper part of the distal face of the elevations, circular and *c.* 4 μm in diameter, surrounded by a narrow hyaline unthickened rim, their areolae in radial rows, *c.* 32 in 10 μm. 3–6 linking spines on the proximal sides of the tips of the elevations, usually expanded above and interlocking with those of the sibling valve, sometimes (on end cells) tapering upwards, *c.* 4 μm long; *c.* 6 short spines *c.* 0·5 μm tall on the distal side of the tips of the elevations. One labiate process on the central portion of the valve 3–5 μm proximal to a sulcus, opposite the centre of the sulcus or, more frequently slightly offset in a clock-wise direction when the valve is viewed from its external side, its inner opening parallel to the sulcus, its outer tube almost vertical to strongly inclined distally with its tip touching the surface of the adjacent projection.

forma **exsculptum** (Figs 1–3, 5, 6, 86, 88)

Valves quadripolar.

Paleocene. Indian Ocean, 14° 46·7′ S., 88° 54·4′ E., 4780 m depth. Vityaz station 6744-40 (Mukhina, 1974, 1976).

Cape basin, South Atlantic Ocean, 29° 29·055′ S., 3° 30·74′ E., 4805 m depth. Deep Sea Drilling Project site 524 (Gombos, 1984).

Paleocene – lower Eocene. Barents Sea, 100–500 m depth, between Franz-Josefs Land and Novaya Zembla (Grunow, 1884). (Date uncertain, more probably Paleocene.)

Lower Eocene. Jutland, Denmark (BM 45388, 45391, 74094; PH coll. Schulze arr. 3192; Benda, 1972).

Glyngøre, Jutland, Denmark (BM 30847).

Skive, Jutland, Denmark (BM 14744, 69223; Tempère & Peragallo, 1891, 1913).

Harre, Jutland, Denmark. Drill hole (Fenner, 1985).

Limfjord, Jutland, Denmark (BM 9840, 13588, 45644, 46747, 54353, 54354, 54515, coll. Adams Bess. 1154; Miller, 1969).

Island of Mors, Denmark (BM 9856, 9857, 10411, 10413, 12927, 14297, 27798, 30863, 31535, 32718, 32719, 38292, 44007, 44008, 44009, 44509, 54351, 54357, 60821, 60822, 60823, 60824, 60825, 60826, 64013, 68374, 68375, coll. Adams Bess. 1788, F1096, GC3483, J587, J2952, SEM CB15.281–289; PH coll. Boyer S-1-18, Gen. coll. 12724; BRM Hd1/12; Heiberg, 1863; Kitton, 1870; Cleve & Möller, 1878; Tempère & Peragallo, 1889*b*, 1907).

Nykjobing, Island of Mors, Denmark (BM 12926, 31604, 54798, coll. Adams C514; Kitton, 1870; Cleve & Möller, 1878).

Ejerslev, Island of Mors, Denmark (BM coll. Adams TS286, TS287, TS416).

Island of Fur, Denmark (BM 10412, 14271, 14272, 27806, 35882, 45389, 53564, 60779, 64014, 68656, coll. Adams Bess. 358, F116, L22, SEM B28.988–991, B29.88–93; PH Gen coll. 10736; BRM Hd1/13; Heiberg, 1863; Kitton, 1870; Tempère & Peragallo, 1889*a*, 1911).

Henmoor, Niedersachsen, Germany (Schulz, 1927).

Dornbusch, Hiddensee, Rostock, Germany (Schulz, 1927).

Greifswalder Oie, Rostock, Germany (BRM 428/70; Schulz, 1927).

London clay, near base (locality not indicated), England (Shrubsole & Kitton, 1881).

Prionersk, Kaliningrad oblast, U.S.S.R. (Strel'nikova, Kaplan & Travina, 1978).

Middle Volga basin, U.S.S.R. (Glezer et al., 1974).

Sengilei, Ulyanovsk oblast, U.S.S.R. (Glezer, 1966).

Region of Atlym, Berezovo, Kazym (i.e. 62°–64° N., 65°–67° E.), Tyumen'sk oblast, U.S.S.R. (Rudkevich, Rubina & Permyakov, 1957; Galerkina, 1959).

North-west of Fergana, Uzbek S.S.R., U.S.S.R. (Glezer et al., 1974).

Middle Eocene. Region of Atlym, Berezovo, Kazym, Tyumen'sk oblast, U.S.S.R. (Rudkevich, Rubina & Permyakov, 1957; Galerkina, 1959).

Junction of rivers Ob and Chemashevskoi, Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Plain between the rivers Ob and Pur, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).

Tazovsk Peninsula, Tyumen'sk oblast, U.S.S.R (Paramonova, 1964).

Middle–upper Eocene. Norwegian Sea, North Atlantic Ocean, 67° 47·11′ N., 5° 23·26′ E., 1297 m depth. Deep Sea Drilling Project site 338 (Dzinoridze et al., 1978).

Upper Eocene. Norwegian Sea, North Atlantic Ocean, 67° 12·47′ N., 6° 18·38′ E., 1217 m depth. Deep Sea Drilling Project site 340 (Dzinoridze et al., 1978).

Chelyabinsk oblast, U.S.S.R. (Proshkina-Lavrenko et al., 1949*b*).

Sverdlovsk oblast, U.S.S.R. (Proshkina-Lavrenko et al., 1949*a, b*).

Ivdel area, well 130, Sverdlovsk oblast, U.S.S.R. (Glezer, 1966).

Serov area, wells 762, 771, Sverdlovsk oblast, U.S.S.R. (Glezer, 1966).

Koptelovo area, well 255, Sverdlovsk oblast, U.S.S.R. (Glezer, 1966).

Luchinkin, Sverdlovsk oblast, U.S.S.R. (Vozzhennikova, 1960).

'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. (BM 35045, 65831, 65832, 78364, coll. Adams TS743, TS748, TS749, SEM B27.529–530, CB13.717–725, CB15.276–280, CB15.368–375, 4106–4116; Chenevière, 1934).

Kimkya, basin of the river Severnaya Sos'va, Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Tyumen', Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Lar'yak, Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Region of Atlym, Berezovo, Kazym, Tyumen'sk oblast, U.S.S.R. (Rudkevich, Rubina & Permyakov, 1957; Galerkina, 1959).

Junction of rivers Ob and Chemashevskoi, Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Nyda, Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Plain between the rivers Ob and Pur, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).

Basin of the Arka-Tab-Yakha, Tyumen'sk oblast, U.S.S.R. (Glezer, 1966).

Tazovsk Peninsula, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).

Pudino, Tomsk oblast, U.S.S.R. (Vozzhennikova, 1960).

Vasyugan, Tomsk oblast, U.S.S.R. (Glezer, 1966).

Parabel', Tomsk oblast, U.S.S.R. (Glezer, 1966).

River Shet-Irgiz, bore no. 6, Kazakhstan, U.S.S.R. (Glezer, 1969).

Region of Ayak-Kuduk, Kazakhstan, U.S.S.R. (Shibkova, 1968).

Region of Kara Tau, Kazakhstan, U.S.S.R. (Shibkova, 1968).

Region of Lake Balkash, Kazakhstan, U.S.S.R. (Shibkova, 1968).

Upper Eocene–Oligocene. Tyumen', Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Lar'yak, Tyumen'sk oblast, U.S.S.R. (Vozzhennikova, 1960).

Lower Oligocene. Eastern slopes of the northern and central Urals – Tyumen'sk and Sverdlovsk oblasts. (Proshkina-Lavrenko et al., 1949*a*).

Northern Urals, Tyumen'sk oblast, U.S.S.R. (BM SEM CB15.264–265, CB15.273–275).

forma **pentagona** Jousé* (Figs 4, 87)

Solium exsculptum [*'exculptum'*] var. *pentagonalis* Kitton ex Walker & Chase, *Notes on some new and rare diatoms* [I]: 5, pl. 1 fig. 10 (1886).

Valves 5-polar.

Paleocene. Cape Basin, South Atlantic Ocean, 29° 29·055′ S., 3° 30·74′ E., 4805 m depth. Deep Sea Drilling Project site 524 (Gombos, 1984).

Lower Eocene. Isle of Mors, Denmark (BM coll. Adams F1096).

Isle of Fur, Denmark (BM 10412; Kitton, 1870; Walker & Chase, 1886).

Upper Eocene. 'Kamichev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R. (BM 65833, SEM CB16.491–495, CB16.789–790).

Plain between the rivers Ob and Pur, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).

Tazovsk Peninsula, Tyumen'sk oblast, U.S.S.R. (Paramonova, 1964).

Lower Oligocene, Northern Urals, Tyumen'sk oblast, U.S.S.R. (BM SEM CB15.260–263, CB15.271–272).

Although both H. L. Smith (1872) and Van Heurck (1896) included *Solium* in *Hemiaulus*, neither of them published the combination *Hemiaulus exsculptus*; this was first done by Schütt

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* We have not been able to trace the valid publication of this name, which is used by Paramonova (1964) but assume that it has been given valid publication in some work not available to us. If not, it is validly published here by the reference given to a validly published varietal name. In this connexion, it should be pointed out that epithets do not have priority outside their own rank.

(1896), whose publication appeared later in the year than Van Heurck's. The specific epithet has frequently been misspelled *'exculptum'* or, in combination with *Trinacria*, *'exculpta'*.

The 5-polar form of this species occurs in a number of localities along with the quadripolar form, although normally less commonly. It has never been recorded in the absence of the quadripolar form. As it does not seem to have a distinct distribution in either space or time, there is no case for separating it taxonomically at a higher rank than forma, but we have recognized it at this level as some authors may wish to note that it is present in material on which they are reporting. The size range of the specimens of this form that we have seen corresponds to the lower part only of the size range of the quadripolar specimens.

Walker & Chase (1886) attribute the name *Solium exsculptum* var. *pentagonalis* to Kitton, saying 'the variety with five angles is mentioned by Kitton', but he did not publish the name; he merely remarked: 'in the Fuur deposit valves with five angles are not uncommon' (Kitton, 1870).

This species shows little variation in any other characters than the number of poles except that specimens with prominent hollow spines or occluded processes occur only in certain localities. These structures are not present on specimens from the lower Eocene of Denmark but are usually to be found on those from 'Kamichev' (presumed to be Upper Eocene from Kamyshlov, Sverdlovsk oblast, U.S.S.R.). A specimen from material received from the late Mr A. L. Brigger and labelled 'North Urals, U.S.S.R. Oligocene' has what appears to be the base of one such spine or occluded process, its upper part, like the external part of the labiate process, having been broken off. The broken base of such a structure may be present on one of the specimens of the tropical Indian Ocean illustrated by Jousé (1977: tabl. 67 fig. 10) and one or two are present on the upper Eocene specimen from the western Siberian lowlands illustrated by Glezer et al. (1974: tabl. 23 fig. 4). None, however, are visible on the illustrations of specimens from the late Paleocene of Cape basin, South Atlantic (Gombos, 1984: pl. 8 figs 9–11), nor on the upper Eocene specimen from NW Siberia illustrated by Paramonova (1964: tabl. X fig. 2).

The end valves (Figs 1, 2), i.e. those not inseparably linked to their sibling valves by interlocking linking spines, differ from the others not only in their linking spines but also in the inclination of the external part of their labiate processes. On the valves within the chain these are so strongly inclined that they almost or quite touch the surface of the projection distal to their point of insertion (Fig. 3); this makes them very difficult to detect when specimens in girdle view are examined with the light microscope. On end valves, however, the external tubes of the labiate processes are inclined at less than 45 degrees to the pervalvar axis, and they may be almost vertical (Fig. 1). The frequency with which end valves are encountered is such as to suggest that the chains in this species were short.

We have seen two lower Eocene specimens from Glyngøre, Jutland, Denmark, that have the appearance of being initial valves. These have sides of 91 μm and 94 μm. The first has no costae delimiting three of its four projections whilst the other is somewhat asymmetrical, two adjacent projections being larger than the other two. Both of these specimens have the labiate process opposite the centre of a side of the valve instead of opposite a projection, the normal position.

The specimens illustrated by A. Schmidt (1890: taf. 152 figs 24–25), of which he says 'nach Witt's Ansicht vielleicht zu *Solium exsculptum* zu rechnen' are not this species but *Trinacria cristata* Gombos (1982). We have examined the specimens that are the originals of these figures (BM coll. Adams J3016 – both specimens are mounted on this slide). Proshkina-Lavrenko et al. (1949*b*) treat *Trinacria semseyi* Pant. as a synonym of *Solium exsculptum* but this is a manifest error. *T. semseyi*, which comes from the upper Eocene of Kuznetsk, Penza oblast, U.S.S.R., is a tripolar species which has the characters of *Trinacria*, not *Solium*.

The earliest records of this species are from the upper Paleocene of the South Atlantic (Gombos, 1984) and the tropical part of the Indian Ocean (Mukhina 1974, 1976). All the subsequent records are from northern Europe or adjacent seas, north-western Siberia, the central Volga basin, and Kazakhstan. It persisted throughout the Eocene in this area, and continued into the lower Oligocene in north-western Siberia. It is not rare in its lower Eocene localities nor in the upper Eocene from north-western Siberia, but elsewhere it is apparently infrequent in its occurrence. This rather peculiar distribution, in low latitudes in the Paleocene and in high northern latitudes from the lower Eocene to the Oligocene, seems more likely to be a reflection of the inadequacy of the fossil record than a complete record of its history. It is presumably because it is only in north-western Siberia that it has been found to occur commonly in the upper Eocene that Fenner (1985) says that it is characteristic for the late Paleocene and earliest Eocene, whereas Glezer (in Glezer et al., 1974: 140) remarks that it did not decrease in the upper Eocene.

A misprint in a previous paper (Ross, Sims & Hasle, 1977) that we have only recently detected suggests that *Solium exsculptum* occurs in Eocene samples from the Falkland Plateau taken by R/V Vema. It does not. The first line of the upper of the two paragraphs on p. 180 of that paper which begins: '*Hemiaulus februatus* and *Trinacria exsculpta* . . .' should read: '*Hemiaulus centralitenuis, H. reflexispinosus*, and *H. prolongatus* from . . .'

We have seen three specimens of this species labelled as coming from localities that we have not included when listing its distribution. These are: PH Gen. coll. 89190, Jackson's Paddock, Oamaru, New Zealand; BM coll. Adams TS478, San Redondo, California, U.S.A. BRM Hd2/27, Santa Monica, California, U.S.A. As there is no other record of the occurrence of this species in any of these much studied deposits, we regard these specimens as strays and have not accepted these records.

II. ***PSEUDORUTILARIA*** (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni, *Syll. Alg.* **2**: 854 (1894).

Subgen. *Pseudo-rutilaria* Grove & Sturt in *J. Quekett microsc. Club* II, **2**: 324 (1886), nom invalid (Arts 21.1, 33.1).

Rutilaria subgen. *Pseudorutilaria* Grove & Sturt ex De Toni & Levi in *Notarisia* **2**: 349 (1887).

Frustules rectangular, united in inseparable chains. Valves bipolar or tripolar, the bipolar valves having a straight or curved apical axis, with long projections each cut off from the central portion by a transverse sulcus or internal costa and crossed by a number of other sulci or internal costae; valve surface undulate. Elevations at each pole not very tall, not expanded above, with a clearly defined subocellus on their distal side, interlocking linking spines at their tip on the proximal side, and anastomosing low external costae on their lower part and on the mantle below them. Mantle with a deep furrow above a narrow hyaline band, the furrow usually continuous around the whole valve but sometimes present only where the valve margin is convex. Areolae irregularly arranged on the valve surface and the upper part of the mantle, each with a simple volate velum. A well-developed marginal ridge, normally bearing many strong marginal spines, these sometimes fused with those of the sibling valve. An irregular ring of occluded processes on the central portion of the valve more or less alternating with troughs with raised margins that clasp the inclined upper parts of the occluded processes of the sibling valve usually present but absent on end valves and often on the shortest valves. One or two labiate processes normally present on the central portion of the valve, more or less on the transapical axis in bipolar species, their internal openings straight or slightly curved and sessile, their external tubes stout and very similar to the occluded processes but reaching to the margin of the sibling valve.

TYPE SPECIES: *Pseudorutilaria monile* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni (loc. cit.).

The first account of this genus was given by Grove & Sturt (1886). This was headed '*Pseudo-rutilaria*. Nov. subgenus', but there was no positive indication of the genus to which it was to be attributed. The statement: 'We have formed this subgenus for the reception of the species described below, which, while resembling *Rutilaria* in other characteristics, is without the central clasping process, so important a feature of that genus', and the fact that the account of it immediately follows that of *Rutilaria*, make it plain that they intended it as a subgenus of that genus. However, the *International Code of Botanical Nomenclature* provides that 'the name of a subdivision of a genus is a combination of a generic name and a subdivisional epithet connected by a term . . . denoting its rank' (Art. 21.1) and that 'a combination (autonyms excepted) is not validly published unless the author definitely indicates that the epithet or epithets concerned are to be used in that particular combination' (Art. 33.1). Grove & Sturt did not give such an indication. They used the name '*Ps.-rutilaria monile*' in the text for the one species that they included in this subgenus, and '*Pseudo-rutilaria monile*' in the legend of the plate on which it is illustrated.

The subgeneric name *Rutilaria* subgenus *Pseudorutilaria* was validly published by De Toni & Levi in 1887, as also was the specific name *Rutilaria monile*. They attributed both to Grove & Sturt and gave a Latin translation of Grove & Sturt's account of the two taxa. De Toni (1894) later treated *Pseudorutilaria* as a genus, attributing this name also to Grove & Sturt. At the same time he validly published the combination *Pseudorutilaria monile* for the type species. Grunow (1887), Tempère & Peragallo (1890), and Schmidt (1893) used the name *Pseudorutilaria monile* earlier than this but did not give the generic name valid publication.

The most striking and unusual feature of *Pseudorutilaria* is the ring of occluded processes and troughs with raised margins that clasp the distal ends of the occluded processes of the sibling valve. This feature is well shown in Fig. 18. The external tubes of the labiate processes resemble the occluded processes and are clasped by the raised margins of the troughs in the same way; they, however, reach the margin of the valve (see Fig. 32), whereas the occluded processes stop short of it.

There are many points of similarity between this genus and *Solium* Heiberg: the subocelli of the two genera resemble each other closely; both have interlocking linking spines on the proximal sides of the elevations and low anastomosing external costae on the elevations and the upper part of the mantle, although these costae are less well developed in *Pseudorutilaria* than in *Solium*; in both there is a concavity of the mantle above a narrow hyaline rim; both have projections cut off from the central portion of the valve by sulci or internal costae, although in *Pseudorutilaria* the projections are crossed by additional transverse sulci or internal costae; both normally have one labiate process inserted towards the margin of the central portion of the valve, with an elongate sessile internal opening and a stout external tube. The two genera are clearly closely related.

In some species of *Pseudorutilaria*, e.g. *P. incompleta* R. Ross & P. A. Sims, the projections are cut off from the central portion of the valve and are crossed by sulci, inward folds of the valve (Figs 39–41). In others, e.g. *P. monile* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni, all the transverse structures are solid internal costae with their free edges laterally expanded and level with the margins of the valve, which itself has an inwardly projecting rim (Figs 11, 12). In *P. hendeyi* R. Ross & P. A. Sims, however, the proximal transverse structures are sulci and the more distal ones are costae (Figs 48–50, 54).

The only species until now added to the genus since its original publication is *Pseudorutilaria monomembranacea* Schrader in Schrader & Fenner (1976: 994). This species, however, has neither terminal elevations with subocelli and interlocking linking spines nor occluded processes and associated clasping troughs. Strel'nikova (in Dzinoridze et al., 1979: 63) erected for this species the new genus *Praecymatosira*, a genus which she considered was related to *Cymatosira* Grun., and this seems to be its correct position.

In this paper we describe five new species of *Pseudorutilaria* from Eocene material from the south-western Atlantic. One of these is the species misidentified by Hajós (1976: 829) as *P. monile* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni. Also, the diatom misidentified as *Eunotogramma weissei* var. *productum* Grove & Sturt by Fenner (1977: 519) is another of the species described here as new.

The genus has so far been found only in middle to upper Eocene, or possibly lowest Oligocene, deposits in the south-western Atlantic, the Tasman Sea, and New Zealand. This suggests that its species may well prove to be useful stratigraphic markers.

Key to the species

1a. Valves tripolar .... 6. ***hendeyi*** (p. 283)
1b. Valves bipolar:
    2a. Central portion pentagonal and with a crenate margin .... 5. ***incompleta*** (p. 282)
    2b. Central portion circular and with an entire margin:
        3a. Margins of the projections crenate or undulate:

4a. Margins of the projections crenate, indented opposite every transverse costa .... 1. ***monile*** (p. 278)
4b. Margins of the projections undulate, undulations more widely spaced than the transverse costae .... 4. ***hannai*** (p. 281)

3b. Margins of the projections with one gibbosity, elsewhere entire:
5a. Gibbosity of the margins of the projections adjacent to the central portion .... 2. ***clavata*** (p. 279)
5b. Gibbosity of the margins of the projections about midway between the central portion and the apex .... 3. ***nodosa*** (p. 280)

1. **Pseudorutilaria monile** (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni, *Syll. Alg.* **2**: 854 (1894).
(Pl. 2, Pl. 12 fig. 89)

'Pseudo-rutilaria' monile Grove & Sturt in *J. Quekett microsc. Club* II, **2**: 324, pl. 18 figs 7–8 (1886), nom. invalid (Arts 21.1, 33.1).
Rutilaria monile Grove & Sturt ex De Toni & Levi in *Notarisia* **2**: 349 (1887).

Valve bipolar, straight, 75–190 μm long, 17–24 μm broad; central portion circular, separated from the projections by transverse costae; projections about half the breadth of the central portion at their proximal ends, tapering very slightly towards the apices, margins crenulate, indented opposite each transapical costa, costae 6–7 μ m apart, laterally expanded at their free edges, which are level with the inwardly projecting valve margin. Height to the top of the elevations 10–14 μm. Linking spines 3–4 on each elevation, extending rather more than half-way around the summits, *c.* 3 μm tall. Areolae poroid, with a slightly raised external rim, diameter *c.* 0·3 μm, scattered over the whole valve surface and the upper part of the mantle, sparser on the central portion than on the projections, where they are *c.* 8 in 10 μm. Ring of *c.* 6 occluded processes on the central portion, absent on end valves. A stout, flattened marginal spine with a serrate tip between each pair of marginal costae, the spines of sibling valves opposite and abutting against one another, but absent on end valves. Labiate process one, situated in the ring of occluded processes on the central portion, more or less on the transapical axis, the labiate processes of sibling pairs of valves on the same side.

Middle Eocene. South-western Atlantic, Falkland Plateau, 49° 52·194′ S., 40° 50·713′ W., 1844 m depth. Deep Sea Drilling Project site 512 (Gombos, 1983).

Upper Eocene. Oamaru, Otago Province, New Zealand (BM 9241, 9242, 11094, 11140, 11164, 11243, 33316 (Jackson's Paddock), 33317 (Jackson's Paddock), 46542, 46577, 46606, 46633, 52709, 52759, 52760, 60842, 63397, 63398, 64687, 65090, 66566, 71539 (lectotype), 74150, 74151, 76748, 77754 (Jackson's Paddock), 77756, 77758 (Allen's Farm), 77760, coll. Adams Bess. 979, C499, G80, G97 (Cormack's Siding), G104 (Cormack's Siding), G624, GC2614, GC3208, J548, J818 (Jackson's Paddock), TS23, TS271, TS292, TS433 (Allen's Farm), TS949 (Bain's Farm, lower), SEM B4.414–415 (Division Hill), B4.425–428 (Division Hill), CB14.200–208, 44519–44537; BRM Ht1/1, Ht1/2, Ht1/3 (Jackson's Paddock); Grove & Sturt, 1886; Schmidt, 1893; Tempère & Peragallo, 1890 (Bain's Farm, Totara); Tempère & Peragallo, 1908 (Bain's Farm); Laporte & Lefébure, 1929; Tsumura, 1964 (Flume Creek).

South-western Atlantic, 49° 48·67′ S, 36° 39·53′ W, 5095 m depth. Deep Sea Drilling Project site 328 (Gombos, 1976).

Upper Eocene–lower Oligocene. South-western Atlantic, Falkland Plateau, 51° 00·28′ S, 46° 58·30′ W., 2589 m depth. Deep Sea Drilling Project site 511 (Gombos & Ciesielski, 1983).

Although this species was described and figured by Grove & Sturt in 1886, the name *Pseudorutilaria monile* that they used for it was not validly published as they did not give valid publication to *Pseudo-rutilaria* as a generic name. As explained above (p. 276), they said that *Pseudo-rutilaria* was a subgenus but nevertheless made the combination with that name and not with *Rutilaria* Grev., which, as they implied but did not definitely state, was the genus of which *Pseudo-rutilaria* was a subgenus. It was De Toni & Levi (1887) who first gave valid publication to a name for the species. It is clear from their protologue that it was based entirely on Grove & Sturt's account and its type material is thus the specimens that those authors had studied.

Although both Grove's and Sturt's collections are in the British Museum (Natural History), none of the specimens in either of them is the original of either of their figures. One cannot say which, if any, were in their hands at the time when their paper was written; some certainly were not. There are a number of other slides mounted by Grove elsewhere in the collections at the Museum, and one of these, BM 71539 from the collection of Thomas Saxton, is a strewn slide from Oamaru labelled in Grove's hand. Amongst the names of species on the label is 'Rut. monile', and it can therefore be regarded as certain that this slide was prepared and labelled before Grove & Sturt published their account of the species and that the specimens on it are part of the original material; on all the other slides labelled by Grove the name is given as *Pseudo-rutilaria monile*. We therefore designate this slide as lectotype.

We have seen under the scanning electron microscope one specimen of this species that we interpret as an end valve. This specimen, which is 120 μm long, has no occluded processes nor troughs on its central portion and it lacks marginal spines.

This species has a known range from the middle Eocene–Oligocene boundary in deposits from the south-western Atlantic and it also occurs in the late upper Eocene deposit at Oamaru, Otago Province, New Zealand, from which it was originally described. The records of it from the upper Eocene of the Tasman Sea by Hajós (1976) are based on a misidentification; the species she illustrated is *Pseudorutilaria clavata* R. Ross & P. A. Sims.

2. **Pseudorutilaria clavata** R. Ross & P. A. Sims, **sp. nov.**
(Pl. 3; Pl. 12 figs 90, 91)

Pseudorutilaria monile sensu Hajós in *Init. Rep. Deep Sea Drilling Proj.* **35**: 829, pl. 14 figs 10–12 (1976), non Grove & Sturt.

Valva bipolaris, recta, 65–155 μm longa, 22–30 μm lata; portio centralis circularis, ab projecturis sulcis transversis separata; projecturae sulcis transitae, utraque margine inter sulcum juxta portionem centralem et proximum gibboso, apices versus primo gradatim angustatatum in apices clavatos rotundatos expansa, margine integro. Duo sulci magis proximales in utraque projectura 10–12 μm distantes, alii 6–8 μm distantes. Altitudo ad vertices elevationum 12–14 μm. Spinae ligantes in utraque elevatione 4–5, circum paullo plus quam dimidium proximalem verticis positae, supra valde expansa, 2·0–3·5 μm altae. Areolae poroides, volis occlusae, extrinsecus margine elevato, diametro *c.* 0·3 μm, in fronte et parte superiori limbi irregulariter dispersae, 6–8 in 10 μm sed in portione centrali distantiores, in latere proximali elevationum carentes vel rarissimae. Areolae subocellorum 40–50 in 10 μm. Annulus ex *c.* 6 processibus occlusis constans in portione centrali, in valvis curtissimis carens. Spinae marginales acutae, eis valvae continguae non oppositae, *c.* 5 in 10 μm. Rimoportula una, in annulo processuum occlusorum et plus minusve in axe transapicali posita, eae valvarum contiguarum idem latus versus extensae. Taenia sola visa (?valvocopula) indivisa, *c.* 8 μm alta, seriebus verticalibus areolarum parvarum *c.* 20 in 10 μm, areolis *c.* 15 in 10 μm.

TYPUS: BM 81136, ex stratis eocaenicis de profundis maris Atlantici australis.

Valve bipolar, straight, 65–155 μm long, 22–30 μm broad; central portion circular, separated from the projections by transverse sulci; projections crossed by sulci, gibbous between the central portion and the next transverse sulcus, distal to this tapering and then expanded to clavate rounded apices, their margins entire. Two proximal transverse sulci on each projection 10–12 μm apart, the others 6–8 μm apart. Height to the top of the elevations 12–14 μm. Linking spines on each elevation 4–5, extending rather more than half-way round the proximal side of the summit of the elevation, strongly expanded above, 2·0–3·5 μm tall. Areolae poroid, occluded by volae, with a slightly raised external rim, diameter *c.* 0·3 μm, scattered over the valve surface and the upper part of the mantle, 6–8 in 10 μm, rather sparser on the central portion, absent or very sparse on the proximal side of the elevations. Areolae of the subocellus 40–50 in 10 μm. Ring of about 6 occluded processes on the central portion, absent in the shortest valves. Marginal spines pointed, not opposite those of the sibling valve, *c.* 5 in 10 μm. Labiate process one, situated in the ring of occluded processes and more or less in the transapical axis, the labiate processes of sibling valves on the same side. The only girdle band seen (? valvocopula) undivided, *c.* 8 μm deep, with vertical rows of areolae, rows *c.* 20 in 10 μm, areolae *c.* 15 in 10 μm.

Middle Eocene. South-western Atlantic, Falkland Plateau, 51° 08′ S., 54° 22′ W., 1525 m depth. Vema cruise 17, core 107, (BM SEM CB12.623–628, CB13.172–173, CB13.313–326, 5861–5878), 50 cm (BM 81137, SEM CB14.098–101, CB14.121–124, CB14.930–931, 44263–44268, 44631–44638), 175 cm (BM 81136).

Middle–upper Eocene. South-western Atlantic, Falkland Plateau, 53° 01′ S., 52° 52′ W., 2880 m depth. Vema cruise 18, core 104, 330 cm (BM SEM CB13.585–594, 5891–5894, 5901–5909).

Upper Eocene. South-western Pacific, South Tasman Rise, 47° 59·84°S, 147° 45·85′ E., 1600 m depth. Deep Sea Drilling Project site 281 (Hajós, 1976).

South-western Pacific, Tasman Sea, 43° 54·60′ S., 154° 16·96′ E., 4750 m depth. Deep Sea Drilling Project site 283 (Hajós, 1976).

This species is easily distinguished from *Pseudorutilaria monile* by the outline of the valve; the margin is gibbous between the proximal sulcus and the next and distal to this it is entire, not crenulate. These characters are well shown on Hajós's figures (1976: pl. 14 figs 10–12), making it obvious that the specimens from the upper Eocene of the south-western Pacific that she identified as *P. monile* are actually *P. clavata*.

The girdle band, probably a valvocopula, shown on Fig. 19, is the only one that we have seen on any member of the genus. It would seem that this band is uninterrupted; all the ends of the three pieces of it appear to be breaks and it would seem that no part is missing.

We have seen two specimens of *Pseudorutilaria clavata* that are about 65 μm long. Both of these consist of two sibling valves inseparably joined by interlocking linking spines on their elevations (Fig. 20). There is one labiate process but no occluded processes on the central portion of each valve of these specimens. It would seem that in this species, as in *P. incompleta* R. Ross & P. A. Sims (see p. 282 below), these structures are not developed on the shortest specimens. There are, however, indications of a ring of tooth-like spines at the centre of the valve similar to those on the end valves of *P. incompleta*, but the position of the specimens does not allow certain observation of this.

Pseudorutilaria clavata has a range from the middle Eocene to the upper Eocene. It has been found in samples from the Falkland Plateau that date from the middle Eocene and from the middle–upper Eocene boundary, and in others from the Tasman Sea area of the south-western Pacific that are upper Eocene in date.

3. **Pseudorutilaria nodosa** R. Ross & P. A. Sims, **sp. nov.**

(Pl. 4; Pl. 12 fig. 92)

Valva bipolaris, recta curvatave, 145–195 μm longa, 32–34 μm lata; portio centralis circularis, ab projecturis costis internis transversis separata; projecturae costis transitae, apices paullo clavatos rotundatos versus gradatim angustatae, sed medio gibbosae, marginibus alibi integris. Costae 7–10 μm distantes, eae medio propriores distantiores. Altitudo ad vertices elevationum *c.* 15 μm. Spinae ligantes 2–4 in utraque elevatione, circum dimidium proximalem verticis positae, *c.* 4 μm altae. Areolae poroides, extrinsecus margine paullo elevato, diametro *c.* 0·3 μm, in fronte et parte superiori limbi irregulariter dispersae, *c.* 6 in 10 μm. Areolae subocellorum 40–45 in 10 μm. Annulus ex 6–7 processibus occlusis constans in portione centrali. Spinae marginales acutae, eis valvae continguae non oppositae, 5–7 μm distantes, sed prope apices crebriores. Rimoportula una, in annulo processum occlusorum et plus minusve in axe transapicali posita, eae valvarum contiguarum idem latus versus extensae.

TYPUS: BM 81138, ex stratis eocaenicis de profundis maris Atlantici australis.

Valve bipolar, straight or curved, 145–195 μm long, 32–34 μm broad; central portion circular, separated from the projections by transverse internal costae; projections crossed by costae, gradually tapering but gibbous about half-way to the slightly clavate rounded apices, margins entire. Transverse costae 7–10 μm apart, those near the apices the more closely spaced. Height to the top of the elevations *c.* 15 μm. Linking spines on each elevation 2–4, extending half-way around the summit on its proximal side, *c.* 4 μm tall. Areolae poroid, with a slightly raised external rim, diameter *c.* 0·3 μm, scattered over the valve face and the upper part of the mantle, *c.* 6 in 10 μm. Areolae of the subocellus 40–45 in 10 μm. Ring of 6–7 occluded processes on the central portion. Marginal spines pointed, not opposite those of the sibling valve, 5–7 μm apart but closer near the apices. Labiate process one, situated in the ring of occluded processes on the central portion and more or less in the transapical axis, the labiate processes of sibling valves on the same side.

Middle Eocene. South-western Atlantic, Falkland Plateau, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107, 50 cm (BM SEM CB15.059–071), 175 cm (BM 81138).

Middle–upper Eocene. South-western Atlantic, Falkland Plateau, 53° 01′ S, 52° 52′ W, 2880 m depth. Vema cruise 18, core 104, 330 cm (BM SEM CB11.813–814, 5879–5883).

? 'Lamont E8'. (Locality and age uncertain, see p. 271) (BM SEM 2715–2728).

The swelling about half-way along each projection is the distinguishing feature of this species, and it is to this that the specific epithet applies. *Pseudorutilaria clavata* is the only other species of the genus in which the margins of the projections are not undulate or crenate. It, too, has a swelling on the projections, but that is situated immediately adjacent to the central portion. In *P. clavata*, also, the transverse structures are sulci, not the costae that are found in *P. nodosa* (Figs 24, 26). None of the specimens of this species that we have seen has any trace of a velum in its areolae.

The certain records of this species are from samples from the Falkland Plateau that date from the middle Eocene and from the middle–upper Eocene boundary. We have also seen specimens from the sample labelled 'Lamont E8', which we believe to come from the same area and to be of about the same age.

4. **Pseudorutilaria hannai** R. Ross & P. A. Sims, **sp. nov.**
(Pl. 5; Pl. 12 fig. 93)

Valva bipolaris, curvata, 150 μm longa, 32 μm lata; portio centralis circularis, ab projecturis costis transversis separata; projecturae costis transitae, ad fines suas proximales latitudine 2/3 ejus portionis centralis, apices angustos rotundatos versus decrescentes, marginibus undulatis, non crenulatis, undis 15–18 μm distantibus. Costae *c.* 8 μm distantes. Altitudo ad vertices elevationum *c.* 13·5 μm. Spinae ligantes 2–3 in utraque elevatione, circum dimidium proximale verticis positae, supra valde expansae, *c.* 4 μm altae. Areolae poroides, extrinsecus margine paullo elevato, diametro *c.* 0·5 μm, in fronte et parte superiori limbi irregulariter dispersae, 6–8 in 10 μm, in portione centrali distantiores. Annulus ex 3–4 processibus occlusis constans in portione centrali. Spinae marginales 2–3 in 10 μm, pro parte maxima clavatae et eis valvae contiguae non oppositae et nonnullae cum eis implexae, aliquae irregulariter formatae positaeque. Rimoportula una, in annulo processuum occlusorum et plus minusve in axe transapicali, positae, in valvis nonnullis carentes.

Typus: BM 81300, ex stratis eocaenicis de profundis maris Atlantici australis.

Valve bipolar, curved, 150 μm long, 32 μm broad; central portion circular, separated from the projections by transverse costae; projections crossed by costae, at their proximal ends about ⅔ the width of the central portion, tapering to narrow rounded apices, their margins undulate, not crenulate, the crests of the undulations 15–18 μm apart. Costae *c.* 8 μm apart. Height to the top of the elevations *c.* 13·5 μm. Linking spines 2–3 on each elevation, extending half-way round the proximal side of the summit, strongly expanded above, *c.* 4 μm tall. Areolae poroid, with a slightly raised external rim, diameter *c.* 0·5 μm, scattered over the valve face and the upper part of the mantle, 6–8 in 10 μm, rather sparser on the central portion. Ring of 3–4 occluded processes on the central portion. Marginal spines mostly clavate and alternating and in places interlocking with those of the sibling valve, 2–3 in 10 μm, but some irregular in shape and arrangement. Labiate process one, situated in the ring of occluded processes, and more or less in the transapical axis, absent on some valves.

Middle–upper Eocene. South-western Atlantic, Falklands Plateau, 53° 01′ S., 52° 52′ W., 2880 m depth. Vema cruise 18, core 104, 330 cm (BM 81300, SEM CB13.595–599, CB13.601–607, 5910–5912).

This species is the rarest of the genus and we have seen only one specimen which we have examined with the scanning electron microscope and then mounted to serve as the type. The undulate outline, which is not related to the position of the transverse costae (Fig. 34), distinguishes it from the other bipolar species. The one specimen that we have seen consists of two joined sibling valves. One of these has one labiate process, the other appears to have no labiate process. We have not seen a specimen of any other species of the genus without a labiate process. This specimen comes from a middle to late Eocene sample from the Falkland Plateau.

5. **Pseudorutilaria incompleta** R. Ross & P. A. Sims, **sp. nov.**
(Pl. 6; Pl. 13 figs 94, 95).

Eunotogramma weissei var. *productum* [*'producta'*] sensu Fenner in *Init. Rep. Deep Sea Drilling Proj.* **39**: 519, pl. 27 figs 3–5 (1977), non Grove & Sturt.

Valva bipolaris, angulo 30°–45° inter projecturas, margine ubique crenulato, 50–155 μm longa, 25–45 μm lata; portio centralis pentagonalis, ab projecturis sulcis transversis sed non indentationibus marginis separata; projecturae sulcis transitae, apices angustos rotundatos versus gradatim angustatae. Sulci 6–7 μm distantes. Altitudo ad vertices elevationum 8·5–11 μm. Spinae ligantes in utraque elevatione 1–2, plerumque supra expansae et implexae, *c.* 2 μm altae, aliquando spina una decrescens *c.* 3·5 μm alta. Areolae poroides, volis occlusae, extrinsecus margine elevato, diametro *c.* 0·3 μ, in fronte et parte superiori limbi irregulariter dispersae, 6–10 in 10 μm. Areolae subocellorum *c.* 50 in 10 μm. Annulus ex 8–12 processibus occlusis constans in portione centrali, aliquando annulo spinarum humilium cuneatarum substitutus, in valvis curtissimis carens. Spinae marginales latae, supra expansae, eas valvae contiguae tangens, margine superiori irregulariter indentatae. Rimoportula una, paullo extra annulum processuum occlusorum et latus dorsale valvae versus posita.

TYPUS: BM 81139, ex stratis eocaenicis de profundis maris Atlantici australis.

Valves bipolar, with the projections at an angle of 30°–45° to one another, margin crenulate throughout, 50–155 μm long, 25–45 μm broad; central portion pentagonal, separated from the projections by transverse sulci but not by indentations of the margin; projections crossed by sulci, gradually tapering to the narrow rounded apices. Transverse sulci 6–7 μm apart. Height to the summit of the elevations 8·5–11 μm. Linking spines 1–2 on each elevation, normally expanded above and interlocking, *c.* 2 μm tall, sometimes a tapering spine *c.* 3·5 μm tall. Areolae poroid, occluded by volae, with a raised external rim, diameter *c.* 0·3 μm, scattered over the valve surface and the upper part of the mantle, 6–10 in 10 μm. Areolae of the subocellus *c.* 50 in 10 μm. Ring of 8–12 occluded processes on the central portion, sometimes replaced by a ring of low cuneate spines, absent in the shortest valves. Marginal spines broad, expanded above, abutting against those of the sibling valve and with irregularly indented upper margins. Labiate process one, slightly outside the ring of occluded processes on its dorsal side.

Middle Eocene. South-western Atlantic, Falkland Plateau, 51° 08′ S, 54° 22′ W, 1525 m depth. Vema cruise 17, core 107 (BM 81139, SEM B26.67–77, B26.645–651), 50 cm (BM 81140, CB14.095–097, CB14.102–110, CB14.125–128, CB14.909–929, CB15.041–057), 170 cm (BM 81141).

South-western Atlantic, south-west edge of the Sao Paulo Plateau, 28° 17·22′ S, 41° 05·28′ W, 3203 m depth. Deep Sea Drilling Project, site 356 (Fenner, 1977).

Middle–upper Eocene. South-western Atlantic, Falkland Plateau, 47° 45·7′ S, 57° 38·5′ W, 3650 m depth. Conrad cruise 12, core 237 (BM SEM 5444–5450, 23545–23554, 33543–33549).

? 'Lamont E8'. (Locality and age uncertain, see p. 271) (BM SEM 2706–2709, 2711–2714, 2729–2730).

Amongst the specimens of this species that we have examined with the scanning electron microscope there are two which differ from the others in a number of ways: the ring of occluded processes and flanged troughs on the central portion is replaced by a rather smaller hyaline area surrounded either by eight or nine low cuneate spines or by a low flange-like costa (Figs 39, 45); the external tube of the labiate process is straight, not curved; the marginal ridge is undulate but bears no spines; there is one spine on each elevation and this is not expanded above but tapers to a point. We interpret these as separation valves. A third specimen consisting of a single valve mounted with its inner side uppermost seems also to be a separation valve. It has a raised (seen as depressed from the inside) area in the centre similar in size to the raised hyaline area of the other two and it has no marginal spines.

On shorter valves neither occluded processes and their associated troughs nor cuneate spines are present on the central portion of the valve. Of specimens we have examined with the light microscope, there is one that is 100 μm in length that has neither, and another of the same length, the holotype, which has a ring of occluded processes and troughs. A further specimen 80 μm long has neither occluded processes nor cuneate spines and there is no sign of any of these on the three specimens figured by Fenner (1977) under the name *Eunotogramma weissei* var. *productum* Grove & Sturt; these are 50 μm, 60 μm, and 80 μm long. *E. weissei* var. *productum* differs from *Pseudorutilaria imcompleta* in a number of ways: it has entire margins; its projections do not taper towards the apices and are much narrower proximally relative to the breadth of the central portion; they are crossed by costae expanded laterally at their free edges; there is a ring of *c.* eight labiate processes on the central portion; the elevations bear pseudocelli but no linking spines. Although neither linking spines nor subocelli can be seen on Fenner's figures, they do not show that the specimens did not possess them, and in all other respects the specimens that she illustrates have the characters that distinguish *P. incompleta* from *E. weissei* var. *productum*; they clearly are the former.

Pseudorutilaria incompleta occurs in samples from the Falkland Plateau and from the south-west edge of the Sao Paulo Plateau that date from the middle Eocene. It also occurs in a sample from the edge of Falkland Plateau (Conrad cruise 12, core 237) the age of which is less well established but is almost certainly middle or upper Eocene. We have also seen specimens from 'Lamont E8', a sample for which there are no firm data but which we believe to come from the Falkland Plateau area and to be of about the same age as the other samples in which the species occurs.

6. **Pseudorutilaria hendeyi** R. Ross & P. A. Sims, **sp. nov.**

(Pl. 7; Pl. 13 fig. 96)

Valva tripolaris, marginibus concavis, crenulatis, 95–185 μm ab apice ad apicem; portio centralis hexagonalis, ab projecturis sulcis transversis sed non indentationibus marginis separata; projecturae apices rotundatos versus angustatae, prope portionem centralem sulcis, apices versus costis, transitae. Sulci costaeque *c.* 8·5 μm distantes. Crenae marginis *c.* 11 μm distantes, eae in lateribus oppositis projecturae non semper oppositae. Altitudo ad vertices elevationum *c.* 10 μm. Spinae ligantes 3–4 in utraque elevatione, supra expansae et implexae. Areolae poroides, diametro *c.* 0·3 μm, in fronte irregulariter dispersae vel in seriebus obliquis indistinctis positae, 6–8 in 10 μm, prope centrum valvae et in parte superiori limbi distantiores vel carentes. Area irregularis diametro *c.* 10 μm ad centrum valvae porellis *c.* 30 in 10 μm instructa. Annulus ex *c.* 12 processibus occlusis constans ad centrum valvae, aream porellorum cingens. Spinae marginales *c.* 4 μm distantes, irregulariter positae, eae valvae contiguae non oppositae, supra dendriticales et hic illic implexae. Rimoportula una vel duae approximatae in annulo processuum occlusorum posita.

TYPUS: BM 81142, ex stratis eocaenicis de profundis maris Atlantici australis.

Valves tripolar, with concave crenulate margins, 95–185 μm from apex to apex; central portion hexagonal, separated from the projections by sulci but not by indentations of the margin; projections tapering to the rounded apices, crossed by sulci grading distally into costae. Sulci and costae *c.* 8·5 μm apart. Crenulations of the margin *c.* 11 μm apart, not always opposite on the two sides of a projection. Height to the top of the elevations *c.* 10 μm. Linking spines 3–4 on each elevation, expanded above and interlocking. Areolae poroid, diameter *c.* 0·3 μm, scattered or in indistinct oblique rows on the valve surface, 6–8 in 10 μm, sparser to absent near the centre of the valve and on the upper part of the mantle. An irregular area, diameter *c.* 10 μm, of porelli *c.* 30 in 10 μm in the centre of the valve. Ring of *c.* 12 occluded processes on the central portion surrounding the area of porelli. Marginal spines *c.* 4 μm apart, irregularly spaced, not opposite those of the sibling valve, dendritically branched above and in places interlocking. One, or two adjacent, labiate processes in the ring of occluded processes.

Middle Eocene. South-western Atlantic, Falkland Plateau, 51° 08′ S., 54° 22′ W., 1525 m depth. Vema cruise 17, core 107, 50 cm (BM 81143, SEM CB14.517–520), 170 cm (BM 81142).

Middle–upper Eocene. South-western Atlantic, Falkland Plateau, 53° 01′ S., 51° 52′ W., 2880 m depth. Vema cruise 18, core 104, 330 cm (BM SEM CB.13.576–584, CB13.617–618, 5884–5890, 5895–5900).

This is the only species of *Pseudorutilaria* with an area of porelli in the centre of the valve (Fig. 51). It would seem that the valve is thinned in this area as it is broken away in most of the specimens we have seen. In none of these is there any trace of vela in the areolae and in all of them the subocelli have been broken away.

Pseudorutilaria hendeyi has only been found in samples from the Falkland Plateau that date from the middle Eocene to the middle–upper Eocene boundary.

III. *MONILE* R. Ross & P. A. Sims, **gen. nov.**

Valvae bipolares, sulcis transitae, ad apices elevationibus munitae. Elevatio utraque annulo ex dentibus radialibus humilibus constanti circum verticem suum instructa et subocellum ferens. Limbus ad apices, centro valvae oppositus et in locis aliquis ubi ambitus valvae convexus est concavus, alibi verticalis. Areolae poroides, cribris occlusae. Rimoportulae paucae, ad centrum valvae irregulariter aggregatae. Taenia sola visa areolata, antiligulam ferens.

SPECIES TYPICA: *Monile laurentii* R. Ross & P. A. Sims, infra.

Valves bipolar, crossed by sulci, with elevations at the apices. Elevations with a ring of radial low teeth around their summits and each bearing a subocellus. Mantle concave at the apices, opposite the centre of the valve and in other places where the outline of the valve is convex, elsewhere vertical. Areolae poroid, occluded by cribra. Labiate processes few, in an irregular group at the centre of the valve. The only girdle band seen areolate, antiligulate.

This genus, like *Pseudorutilaria monile* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni, has something of the appearance of a row of beads. We have therefore chosen as its generic name the noun used in apposition as a substantival epithet for that species, a word meaning necklace.

Monile resembles *Pseudorutilaria* in many ways but differs in important respects: its cells are not united in inseparable filamentous colonies, although the flattened summits of the elevations suggest that they did form filaments (Figs 63, 64); there are no occluded processes with their associated troughs at the centre of the valve (Fig. 61); there are no interlocking linking spines on the elevations (Figs 63, 64); also the subocelli extend on to the summits of the elevations. *Pseudorutilaria* is found earlier in the fossil record than *Monile*, and the nature and degree of the relationship between the two is far from clear. It is discussed below (p. 291).

1. **Monile laurentii** R. Ross & P. A. Sims, **sp. nov.**
(Pl. 8; Pl. 13 figs 97, 98)

Valva bipolaris, longa angustaque, marginibus sinuosis, apicibus subclavatis, ex portione centrali circulari tholiformi et projecturis ab portione centrali sulcis separatis, sulcis transitis et inter sulcos tholiformibus, constans, elevatione ad apicem utremque munita, 63–220 μm longa, 20–25 μm lata. Elevationes verticales, cylindricae, supra expansae, verticibus applanatis, utraque annulo ex dentibus humilibus radialibus linearibus constanti circum verticem instructa, et subocellum in vertice et in parte superiori expansa ferens. In utraque elevatione sub subocello costae humiles irregulariter anastomosantes, reticulum debiliter effectum facientes. Altitudo ad vertices elevationum 18–40 μm. Limbus ad apices, centro valvae oppositus et proximaliter sed non distaliter in projecturis ubi ambitus valvae convexus est, proxime super marginem concavus, alibi verticalis. Crista marginalis humilis, hyalina ab elevationibus ad portionem centralem extensa. Areolae poroides, cribris occlusae, extrinsecus margine paullo elevato, diam. *c.* 0·7 μm, in fronte, in elevationibus et in parte superiori limbi ubi ambitus valvae convexus est irregulariter dispersae, 4–6 in 10 μm; areolae subocellorum 15–20 in 10 μm, diametro *c.* 0·1 μm. Pori interstriales in fronte irregulariter dispersi. Spinae superficiales ad 4 μm longae in fronte praeter partes distales projecturarum, ex marginibus elevatis areolarum orientes. Rimoportulae 4, ad centrum valvae irregulariter aggregatae, unaquaeque apertura interna recta paullo elevata et, extrinsecus, ex tubo crasso 4 μm minimum alto et, pro parte maxima, basi fultura munito constans. Taenia sola visa *c.* 8 μm alta, ad unum apicem antiligula valida instructa, seriebus verticalibus areolarum ornata, seriebus areolisque 10–12 in 10 μm.

TYPUS: BM coll. Adams H941, specim. I, 12, ex depositione miocenica ad 'St. Laurent-la-Vernède', Gard, Gallia.

Valve bipolar, long and narrow, with sinuous margins and sub-clavate apices, consisting of a circular domed central portion separated by sulci from the projections that are themselves crossed by sulci and domed between them, and with an elevation at each apex, 63–220 μm long, 20–25 μm broad. Elevations vertical, cylindrical, expanded above, with flattened summits bearing a ring of low radial linear teeth around their margins, and with a subocellus on their summits and expanded upper part. A poorly developed network of low, irregularly anastomosing costae on the elevations. Height to the top of the elevations 18–40 μm. Mantle strongly concave immediately above the margin at the apices, opposite the centre of the valve and proximally but not distally on the projections where the outline of the valve is convex, elsewhere vertical. A low hyaline marginal ridge extending from the elevations to the central portion. Areolae poroid, occluded by cribra, with a slightly raised external rim, diameter *c.* 0·7 μm, scattered over the valve surface, the elevations, and the upper part of the mantle where the valve outline is convex, 4–6 in 10 μm; areolae of the subocelli 15–20 in 10 μm, diameter *c.* 0·1 μm. Scattered interstrial pores on the valve surface. Superficial spines up to 4 μm long arising from the raised rim of the areolae on the valve surface, except on the distal parts of the projections. Labiate processes 4, in an irregular group in the centre of the valve, each with a straight, slightly raised internal opening and, externally, a stout tube at least 4 μm tall, mostly with a single buttress at the base. One girdle band seen, about 8 μm deep, with a well developed antiligula at one apex and with vertical rows of areolae, rows and areolae 10–12 in 10 μm.

Miocene. St Laurent-la-Vernède, Gard. France (BM 81303, coll. Adams H941, TS961, SEM CB13.634–650, 36674–36682).

IV. ***MALUINA*** R. Ross & P. A. Sims, **gen. nov.**

Valva bipolaris, ad apices elevationibus aliquanto crassis, non supra expansis, ad summum utraeque elevationis in latere suo distali subocello minimo. Limbus verticalis. Areolae poroides, parvae, in partibus valvae sparsae carentesve. Spinae ligantes 2–4 in latere proximali verticis utraeque elevationis, supra expansae et implexae. Rimoportula una, prope centrum valvae posita, infra sessilis longa angusta, extra tubo curto recto.

Species typica: *Maluina centralitenuis* (R. Ross & P. A. Sims) R. Ross & P. A. Sims, comb. nov. infra.

Valve bipolar, with moderately stout elevations at the apices, not expanded above. On the distal side of the top of each elevation a very small subocellus. Mantle vertical. Areolae poroid, small, sparse or absent on parts of the valve. Linking spines 2–4 on the proximal sides of the summits of each elevation, expanded above and interlocking. Labiate process single, situated near the centre of the valve, internally sessile, long and narrow, externally with a short, straight tube.

We have chosen a name for this genus from the only locality where it has been found, the Falkland (Malvinas) Plateau.

It is clear that the species for which this genus is erected here cannot be retained in *Hemiaulus* Heiberg. The interlocking linking spines and, even more obviously, the subocellus with its very close areolae or porelli and its definite margin are inconsistent with that position for it. Also, it cannot be transferred to any of the other genera with a small number of interlocking linking spines on each elevation. *Briggera* R. Ross & P. A. Sims and *Dicladiopsis* De Toni have pseudocelli with indefinite margins and expanded tips to their elevations; *Solium* Heiberg and *Pseudorutilaria* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni have projections cut off from a central portion by sulci or costae, an indented mantle, and anastomosing costae on the elevations and mantle. These differences, in our view, preclude placing *Hemiaulus centralitenuis* R. Ross & P. A. Sims in any of these genera.

1. **Maluina centralitenuis** (R. Ross & P. A. Sims) R. Ross & P. A. Sims, **comb. nov.** (Pl. 9)

Hemiaulus centralitenuis R. Ross & P. A. Sims in *Beih. Nova Hedwigia* **54**: 182, pl. 2 figs 7–9 (1977).

Valves elliptical, 20–55 μm long, 15–25 μm broad, 10–12 μm tall at the domed centre, with more or less strongly developed acute pseudo-antiligulae at the apices and a domed centre about ⅔ the width of the valve in diameter. Elevations arising at the apices, cylindrical and tapering slightly upwards, *c.* 5 μm in diameter; height to the top of the elevations 15–25 μm. Valve surrounded by a flange-like marginal ridge. Areolae poroid, with a weak external rim, *c.* 0·15 μm in diameter, in radial rows on the central dome and sometimes also around the outer part of the valve face, rows 25–30 in 10 μm, areolae 30–35 in 10 μm; areolae also dense, 25–30 in 10 μm, on the distal side and the lower part of the proximal side of the elevations, elsewhere on the elevations sparse; areolae absent in a broad area around the central dome. A very small, transversely widened subocellus on the distal side of each elevation at its tip, the areolae or porelli *c.* 60 in 10 μm. Linking spines 2–4, interlocking, expanded immediately above their base, narrowed above this and then expanded into a clavate tip rounded at the apex, 6–7 μm long. Labiate process about half-way between the centre of the valve and the edge of the central dome, slightly nearer one apex than the other.

Middle Eocene. South-western Atlantic, Falkland Plateau, 51° 08′ S., 54° 22′ W., 1525 m depth. Vema cruise 17, core 107, 50 cm (BM SEM CB14.074–077, CB14.080–083, CB14.502–505, 5818–5826; Ross, Sims & Hasle, 1977).

Middle–upper Eocene. South-western Atlantic, Falkland Plateau, 53° 01′ S., 52° 52′ W., 2880 m depth. Vema cruise 18, core 104, 330 cm (BM 78000, holotype; Ross, Sims & Hasle, 1977).

Since we first described this diatom as a species of *Hemiaulus* (in Ross, Sims & Hasle, 1977), we have been able to examine additional, and less eroded, specimens with the scanning electron microscope. These have provided us with more information about the structure of the valves and hence we have provided a new description here. In 1977 we drew attention to the small area at the tips of the elevations that was broken away in the specimens that we had then seen and suggested that a pseudocellus might have been present there. We now know that this area is occupied by the structure of the sort which we have here called a 'subocellus' (Fig. 68).

This species, and genus, is known only from cores taken from the Falkland Plateau. The samples in which it has been found come from the middle Eocene and the middle–upper Eocene boundary.

V. *BONEA* R. Ross & P. A. Sims, **gen. nov.**

Frustula rectangularis, in catenis inseparabilibus conjuncta. Valvae tripolares, ad apices elevationibus humilibus. Elevatio unaquaeque vertice annulo perfecto spinarum ligantium implexarum circumcincto, et pseudocellum ferens. Limbus verticalis. Areolae poroides, rotis occlusae. Rimoportulae paucae, prope centrum valvae positae. Cingulum ex taeniis duis areolatis, probabiliter indivisis constans.

Species typica: *Bonea simulans* R. Ross & P. A. Sims, infra.

Frustules rectangular, united in inseparable chains. Valves tripolar, with low elevations at the corners. Elevations with their summits surrounded by a complete ring of interlocking linking spines, and bearing a pseudocellus. Mantle vertical. Areolae poroid, occluded by rotae. Labiate processes few, situated near the centre of the valve. Girdle bands two, areolate, probably undivided.

We have named this genus after Mr E. C. P. Bone of Portslade, who has assisted us materially by providing us with many selected specimens of species that we have studied.

Bonea has many points of resemblance to *Strelnikovia* R. Ross & P. A. Sims (1985) but differs in having a complete ring of interlocking linking spines on the summits of the elevations (Figs 73, 75). These linking spines, moreover, have bases that extend circumferentially, not radially as in *Strelnikovia*; in this, *Bonea* resembles more closely *Briggera* R. Ross & P. A. Sims (1985) and *Dicladiopsis* De Toni (1894). *Keratophora* Pantocsek (1889) and *Thaumatonema* Greville (1863), which, like *Bonea*, have a complete ring of interlocking linking spines around the summits of their elevations, also have the bases of these extending radially, as in *Strelnikovia*. The tall, tubular, hyaline elevations of these two genera distinguish them even more sharply from *Bonea*, which, nevertheless, is related to the group of genera that consists of them along with *Strelnikovia, Briggera,* and *Dicladiopsis*.

1. **Bonea simulans** R. Ross & P. A. Sims, **sp. nov.**
(Pl. 10; Pl. 13 figs 99, 100)

Valva tripolaris, lateribus rectis vel paullo convexis, fronte ad centrum paullo tholiformi, inter centrum et medium uniuscuiusque lateris convexa, elevationes versus concava et ad vertices earum ascendenti; longitudo lateris 115–125 μm. Elevationes sub-triangulares, interdum a limbo depressione angusta horizontali separatae. Altitudo ad vertices elevationum *c.* 30 μm. Spinae ligantes in unaquaeque elevatione 15–20, supra expansae et ambitu irregulari. Crista marginalis humilis, hyalina ab elevatione ad elevationem extensa, spinas marginales acutas, 10–12 μm altas, *c.* 5 μm distantes ferens; hae spinae oppositae et superimpositae sed non implexae. Areolae poroides, rotis radiis 7–10 instructis occlusae, radiis ramulo uno vel ramulis duobus conjunctis, diametro 0·8–1·5 μm, in fronte in seriebus radialibus dispositae, seriebus 2·5–4 in 10 μm, areolis 2–4 in 10 μm, sed prope centrum valvae distantiores; series areolarum media laterum versus distantiores quam eae apices versus directae; medio in valva area hyalina irregularis, diametro *c.* 10 μm; in limbo prope marginem series una horizontalis areolarum 2·5–3 in 10 μm et, prope cristam marginalem, alter series similaris. Pori interstriales in fronte irregulariter dispersi. Pseudocellus in vertice et latere distali uniuscuiusque elevationis et in limbo sub elevatione, interdum area hyalina verticali in limbo et, quum depressio horizontalis inter limbum et elevationem adest, area hyalina super hanc interruptus; areolae pseudocellorum in seriebus dispositae, seriebus in vertices elevationum plus regularibus quam alibi; series areolaeque 8–10 in 10 μm; areolae in vertices elevationum diametro 0·2–0·4 μm, minor quam eae alibi diametro 0·5–1·0 μm. Rimoportulae 2–4, prope aream centralem hyalinam irregulariter dispositae, unaquaeque apertura interna recta, curta, paullo elevata, extrinsecus ex tubo verticali *c.* 6 μm alto appendice acuta lanceolata ad apicem instructo constans. Valvocopula parte exteriori *c.* 20 μm alta, ad omnes apices antiligula rotundata humili instructa, et areolis irregulariter dispersis 2·5–4 in 10 μm ornata; pleura parte exteriori *c.* 10 μm alta et parte interiori hyalina *c.* 4 μm alta, pars exterior serie areolarum *c.* 5 in 10 μm secus marginem proximalem et, huic distalibus, seriebus duabus paullo irregularibus areolarum *c.* 4 in 10 μm.

TYPUS: BM 81301, ex stratis eocaenicis ad 'Carlovo, U.S.S.R.'

Valve tripolar, with straight or slightly convex sides, the face slightly domed in the centre, convex between the centre and the middle of each side but concave towards the elevations and rising to their summits, length of side 115–125 μm. Elevations sub-triangular, sometimes separated from the mantle by a narrow horizontal depression. Height to the summit of the elevations *c.* 30 μm. Linking spines 15–20 on each elevation, expanded and rather irregularly shaped above, 2–4 μm tall. A low hyaline marginal ridge running from elevation to elevation and bearing acute marginal spines 10–12 μm tall and *c.* 5 μm apart, the spines opposite and overlapping but not interlocking. Areolae poroid, occluded by rotae with 7–10 spokes, the spokes connected by one or two side branches, diameter 0·8–1·5 μm; radial rows of areolae on the valve face, rows 2·5–4 in 10 μm, areolae 2–4 in 10 μm, except near the centre of the valve, where they are sparser; the rows directed towards the middles of the sides more widely spaced than those directed towards the apices; an irregular central hyaline area *c.* 10 μm in diameter. Mantle with a horizontal row of areolae 2·5–3 in 10 μm close to the margin and another close to the marginal ridge. Scattered interstrial pores on the valve surface. Pseudocellus on the summit and distal face of the elevations and on the mantle below the elevations, where it is sometimes interrupted by a vertical hyaline area, a hyaline area also above the transverse furrow separating mantle and elevation when this is present; areolae of the pseudocelli arranged in rows, more regular on the summits of the elevations than elsewhere, rows and areolae 8–10 in 10 μm; areolae on the summits of the elevations 0·2–0·4 μm in diameter, smaller than those on the distal face and the mantle, which are 0·5–1·0 μm in diameter. Labiate processes 2–4, irregularly distributed a little outside the central hyaline area, with a slightly raised, short, straight internal opening and, externally, a vertical tube *c.* 6 μm tall with a lanceolate acute appendage on its tip *c.* 2 μm long. Valvocopula with a pars exterior *c.* 20 μm deep, with a slightly rounded antiligula at each apex and irregularly scattered areolae 2·5–4 in 10 μm; pleura with a pars exterior *c.* 10 μm deep and a hyaline pars interior *c.* 4 μm deep, the pars exterior with a row of areolae *c.* 5 in 10 μm along its proximal edge and two somewhat irregular rows *c.* 4 in 10 μm distal to this.

? Lower Eocene. 'Carlovo'. U.S.S.R. (BM 81301, SEM 25006–25016, 36571–36580). (For this locality see Ross & Sims 1985: 281)

Bonea simulans resembles *Triceratium exornatum* Greville (1865), which was described from the Cambridge Estate, Barbados; it also occurs in samples from Springfield and Joe's River on that island. The material from the Cambridge Estate has been dated as middle Eocene and that from Joe's River as coming from the upper Eocene–Oligocene boundary (Holmes & Brigger, 1979). There is no firm date available for the material from Springfield. We have examined the holotype of *T. exornatum* (BM 3079) and a number of other specimens of the species with the light microscope but have found no trace of linking spines or marginal spines on any of these. There are a few other minor differences: the areolae of *T. exornatum* are 4·5–5 in 10 μm on the parts of the valve surface between the centre and the elevations, whereas those of *B. simulans* are 3–4 in 10 μm on that part of the valve; there is only one row of areolae on the mantle in *T. exornatum*, but two in *B. simulans* (Fig. 74); in *T. exornatum* a transverse furrow separating elevation from mantle is never present; we could not detect any labiate process on *T. exornatum*. These are the only differences between the species; in outline and contour, in shape of the elevations, in arrangement of the areolae, and in the position and size of the pseudocelli they are alike. We have chosen the epithet *simulans* for the species described here because of this resemblance. It should, perhaps, be pointed out here that *T. exornatum* is not correctly placed in the genus *Triceratium* Ehrenberg (1839). It belongs either in *Sheshukovia* Glezer (1975) or in *Biddulphia* Gray (1821); we have reservations about whether these two genera are distinct.

As we said earlier (Ross & Sims, 1985: 281), there is uncertainty about the locality from which the material labelled 'Carlovo' came and about its geological age. This is the only deposit in which we have found *Bonea simulans*.

Glezer (in Glezer et al., 1974) records *Triceratium exornatum* from the early to late Eocene of the west Siberian plain (pp. 112, 118, 119, 122, tabl. XXI fig. 1) and from the late Eocene of Kazakhstan (pp. 127, 129, tabl. XXXII fig. 8). The two figures are of the same specimen, that on tabl. XXXII rotated 120° anti-clockwise as compared with that on tabl. XXI. It is impossible to tell from these illustrations whether the specimen shown is *T. exornatum* or *Bonea simulans*; it might be either.

VI. ***DEXTRADONATOR*** R. Ross & P. A. Sims in *Bacillaria* **3**: 115 (1980).

Additional information about *Dextradonator eximius* (Grunow) R. Ross & P. A. Sims, the type species of this genus, is given in the description below.

1. **Dextradonator eximius** (Grunow) R. Ross & P. A. Sims in *Bacillaria* **3**: 118, figs 1–4 (1980). (Pl. 11)

Syringidium eximium Grunow in Van Heurck, *Syn. Diat. Belg.*: pl. 106 figs 1, 3 (1883).

Frustules cylindrical, united in inseparable chains, the apical axis 3–10 times as long as the diameter. Valves circular or almost so, the surface flat to concave, diameter 30–75 μm, height to the centre of the valve 20–30 μm. Elevations two, marginal, cylindrical, 5–12 μm in diameter, height to the top of the elevations 55–75 μm. A hyaline marginal ridge *c.* 10 μm tall and turned inwards along its upper edge extending from elevation to elevation. Mantle vertical, hyaline. Areolae poroid, *c.* 0·8 μm in diameter, vela eroded on all specimens seen, in radial rows on the valve surface, rows and areolae 9–10 in 10 μm, extending up the proximal side of the elevations; a few small areolae or pores, 0·2–0·4 μm in diameter on the distal side of the elevations near their summits. An irregular hyaline area containing 1–3 areolae in the centre of the valve, diameter 4–6 μm. Two flattened, acute linking spines on each elevation, partially encircling the elevation of the sibling valve, those on one of a pair of sibling valves arising from the distal side of the tops of the elevations, those on the other from the proximal side, linking spines 15–30 μm tall. No labiate process seen. Cingulum consisting of two entire bands; the valvocopula 60–75 μm deep, its pars interior hyaline and overlapping a rounded internal ridge at the margin of the valve, its pars exterior with a hyaline distal margin 2–5 μm deep, elsewhere with scattered large areolae *c.* 2 μm in diameter and 3–5 μm apart; pleura hyaline, 15–30 μm deep.

Middle Eocene. Cambridge Estate, Barbados (BM 10453, 13789; Grunow in Van Heurck, 1883).
Middle–Upper Eocene boundary. Indian Ocean, 10° 25′ S, 63° 15′ E, 3115 m depth, dredge sample. Dodo-123-D1 (BM SEM B26.387–392, CB11.301–302, CB19.911–912, 46522–46532).
Middle Eocene–lower Miocene. Barbados (BM coll. Adams TS 266; PH coll. Shulze arr. 196, 1352, 2404, 2406, 2791).
Bissex Hill, Barbados (BM coll. Adams TS 891).
Malvern Hill, Barbados (PH coll. Febiger 83, 131).
Mount Hillaby, Barbados (BM coll. Adams GC 3088).
Newcastle, Barbados (BM coll. Adams F 1236).

Since we published our previous account of this species (Ross & Sims, 1980), we have been able to examine more specimens and to add appreciably to our knowledge of it. The most remarkable feature is the inflexed marginal ridge (Fig. 84). This is also present in *Dextradonator jeremianus* R. Ross & P. A. Sims, the other species of the genus, but we know of nothing similar in any other genus.

The stratigraphic range of this species is uncertain. All the specimens that can be firmly dated come from the middle Eocene or the middle–upper Eocene boundary, but there can be no certainty about the level in the Oceanic Beds from which come the specimens from Bissex Hill, Malvern Hill, Mount Hillaby, and Newcastle, and those with no locality detail other than 'Barbados'.

In addition to the specimens that we have definitely identified as *Dextradonator eximius*, there is one about which we are uncertain (Figs 82, 83). This comes from the Indian Ocean dredge sample that dates from the middle–upper Eocene boundary. It has a diameter of 94 μm, appreciably larger than those about whose identity we are sure, and it differs from them in having a marginal ridge that is not turned inwards at its upper edge and that bears two flattened spines about 30 μm tall opposite each other and half-way between the elevations. In all other respects it is identical with the specimens that we include in *D. eximius* with certainty. To decide whether it represents a separate species or whether the characteristics peculiar to it are those of specimens at the upper end of the size range of *D. eximius* needs a greater range of specimens than those currently available to us.

Discussion

As we pointed out in the introduction to this paper, we deal here with a number of genera that do not form a closely related group, and hence their affinities and position in the classification system of diatoms can only be discussed piecemeal. There are, however, a few general points to be made before doing this. As all the genera dealt with in this paper belong to the order Biddulphiales, we need to say something about the position and circumscription of this order. Very different views on this have been put forward during the last decade.

This is not the place to consider whether a taxon containing all the diatoms should have the level of a division or of a subdivision within the Chrysophyta, but the latter is, in our view, the lowest rank to be assigned to it. Some authors, the latest of them Round (1981), have considered that, at the next lower level, the diatoms should be divided into three groups: the centric ones, the pennate ones without a raphe, and those with a raphe. Others, most recently Simonsen (1979), consider that the pennate diatoms with and without a raphe should not be separated at this level. This difference of opinion does not, however, affect the circumscription of a taxon containing the centric diatoms, which include the Biddulphiales. Hendey (1964), on the other hand, rejects the separation of the centric and pennate diatoms, and divides the diatoms into a number of groups with the rank of suborder.

We accept that the centric and pennate diatoms should be separated as distinct taxa at the level of class. Whether the pennates should constitute a single class or two, one without and one with a raphe, is not relevant here. Within the class Centrophycidae we include an order Biddulphiales. We thus agree with Glezer (1979) and Round (1981) about the rank of a taxon that includes *Biddulphia* but excludes *Thalassiosira, Coscinodiscus, Aulacodiscus,* and *Rhizosolenia*, rather than with Simonsen (1979), for whom it is a suborder within the order Centrales.

For both Glezer and Round, the Biddulphiales have a much narrower circumscription than that attributed to his suborder by Simonsen; they both include in the order only part of the Biddulphiaceae as delimited by Simonsen, to which Glezer adds a few genera included by Simonsen in the Eupodiscaceae and the Diatomaceae. We would argue for a much wider circumscription of the order than either Glezer's or Round's, but a somewhat narrower one than Simonsen's in that we consider that the Lithodesmiaceae should not be included. Also, we are not completely certain that either the Chaetoceraceae or the Stictodiscoideae belong in the order. There has, in addition, been one important change in the classification of the genera that we would definitely include within the Biddulphiales: the establishment of the family Cymatosiraceae Hasle, von Stosch & Syvertsen (1983). We point out below the difficulties in classifying into families the remaining genera that we include in the order.

We regard all the diatoms that we definitely include in the Biddulphiales as having polar valves, from unipolar, as in *Isthmia* Agardh, to multipolar, as in those species of *Triceratium* Ehrenberg for which De Toni (1894) erected the genus *Nothoceratium*. We consider that the ocelli of such genera as *Euopodiscus* J. W. Bailey and *Rattrayella* De Toni indicate that the basic morphology of these genera is polar in spite of their circular outline. Also, almost invariably throughout the order as we delimit it the internal opening of the labiate process is straight and projects as no more than a papilla into the interior of the frustule; it is not borne on a stalk as in the Thalassiosirales and Coscinodiscales. The only exceptions of which we are aware are *Isthmia* Agardh (see Navarro, 1981) and *Biddulphiopsis* von Stosch & Simonsen (1984), in both of which the labiate process is shortly stalked internally. Labiate processes of a similar form to that found in the Biddulphiales occur in some Melosiraceae, and all those found in pennate diatoms are of this type. Another character that is widespread among the Biddulphiales as we delimit them is the presence of interstrial pores. The genera in which these occur include not only *Biddulphia* (see Ross & Sims, 1971: pl. 1 fig. 2) and *Biddulphiopsis* (see von Stosch & Simonsen, 1984), but also *Hemiaulus* (see Ross, Sims & Hasle, 1977: pl. 5 fig. 32, pl. 8 fig. 52), *Trigonium* (see Ross & Sims, 1971: pl. 2 fig. 6), *Amphitetras*, and *Pseudauliscus* (unpublished observations). They do not seem to occur, however, in the Cymatosiraceae or the Chaetoceraceae, nor outside the Biddulphiales.

Glezer (1979) restricts the order Biddulphiales to genera with poroid areolae, maintaining that the type of areola is of primary importance in the classification of the diatoms and that such structures as the ocellus and the pseudocellus are polyphyletic (see also Glezer, 1983). She accordingly maintains *Zygoceros* Ehrenberg, a genus with ocelli and loculate areolae (see Ross & Sims, 1971), as separate from *Odontella* Agardh, with ocelli but poroid areolae, whereas other authors, e.g. Simonsen (1974), have included the species with loculate areolae in *Odontella*. She places *Zygoceros*, along with *Trigonium* Cleve, which has loculate areolae but pseudocelli at the apices, in the Coscinodiscaceae, whilst assigning *Odontella* and *Amphitetras* Ehrenberg, another genus with ocelli and poroid areolae, to the Biddulphiaceae, along with *Biddulphia* Gray which also has poroid areolae but has pseudocelli at the apices. The number of characters shared by the genera we include in the Biddulphiales and not present in *Coscinodiscus* Ehrenberg and its obvious allies indicates that this separation on *a priori* grounds is unsound. All the evidence seems to point to loculate areolae being polyphyletic, and the fact that, when areolae become close-packed, they must be of this type for mechanical reasons, reinforces this view. More recently, Glezer (1986) has proposed a new monotypic family for *Triceratium* Ehrenberg *sensu stricto*, and assigned it to the Pyxidiculales. She bases her arguments for this on the view that the pseudoloculi of *Triceratium* are areolae. However, as we showed earlier (Ross & Sims, 1971), and Miller & Collier (1978) confirmed, the pseudoloculi of *Triceratium* are formed by a network of external costae laterally expanded at their free edges and the areolae are small and poroid. The genus is closely related to *Amphitetras*, which Glezer (1979) includes in the Biddulphiales.

As well as differing from Glezer on the circumscription of the Biddulphiales, we also do not agree with her classification of the genera that she includes within the family Biddulphiaceae. She separates the Biddulphiaceae into two subfamilies, one containing those genera with bipolar valves, the other those genera with tripolar and multipolar valves, again on *a priori* grounds.

There is, however, overwhelming evidence that the change from bipolar valves to tripolar ones has happened many times. The range of morphological variation in diatoms of the two shapes is very similar and there are many cases where the only differences between species other than the number of poles are in the detail of the arrangement and spacing of the areolae, characters that in any other context would be regarded as indicating separation at no more than the specific level. There are even a number of cases where bipolar and tripolar forms have been treated as varieties of the same species, *Odontella retiformis* (A. Mann) von Stosch (1985) being the most recent. *Pseudorutilaria* adds another example where bipolar and tripolar diatoms must be considered as belonging to the same taxon at the generic level.

There is a nomenclatural point that must also be considered before discussing the relationships of the genera described above. The family name Eupodiscaceae has long been used in the sense of a family based on the genus *Eupodiscus* J. W. Bailey, nom. cons., published in 1851. However, the family name was published by Kützing in 1849 and is based on *Eupodiscus* Ehrenberg, nom. rej., the type of which is *Eupodiscus germanicus* (Ehrenberg) Ehrenberg, a synonym of *Aulacodiscus argus* (Ehrenberg) A. Schmidt. Eupodiscaceae is thus not the correct name for a family within the Biddulphiales. It is also an illegitimate name because *Eupodiscus* Ehrenberg is not only a rejected name but also an illegitimate superfluous substitute for *Tripodiscus* Ehrenberg.

Solium and *Pseudorutilaria* resemble each other in most respects. The only basis for generic distinction between them is the presence in *Pseudorutilaria* of the troughs on the central portion, the raised edges of which grasp the occluded and labiate processes of the sibling valve. These we regard as a derived feature, and hence we postulate that *Pseudorutilaria* evolved from an ancestor which would, if it were known, be placed in, or very close to, the genus *Solium*.

Whilst the fact that the subocelli of *Solium* and *Pseudorutilaria* consist of areolae and not porelli suggests that their affinities are with *Biddulphia* and *Briggera* rather than with *Amphitetras* and *Odontella*, many of their characters point in the other direction. Their mantles are concave, at least in part, as in *Odontella* and *Amphitetras*, not vertical as in *Briggera* and most species of *Biddulphia*, including its type. Anastomosing low external costae, such as occur on the elevations and mantles of *Solium* and *Pseudorutilaria*, are present throughout on *Amphitetras* but do not occur on *Biddulphia* or any of its allies. On the other hand, no species with a true ocellus has linking spines or internal costae. What is clear, however, is that *Solium* and *Pseudorutilaria*, in spite of their possession of linking spines, are not to be included in the Hemiauloideae sensu Sims (1986).

The only genus that might be close to *Solium* and *Pseudorutilaria* is *Monile*. It closely resembles *Pseudorutilaria* in its shape of valve, in the many sulci crossing its projections, in the concavity of the valve mantle where the valve margin is convex, in the anastomosing costae on its elevations, in the arrangement of its poroid areolae, and in the presence of a subocellus. On the other hand, its areolae are occluded by cribra, not volae. It is only presence of a subocellus rather than a pseudocellus on its elevations, the flattened summits of these, and the ring of radial ridges on them that distinguishes it from *Biddulphia*, although the concavity of the mantle is unusual in that genus. The radial ridges on the summits of the elevations have the same pattern of arrangement as the linking spines of *Strelnikovia* R. Ross & P. A. Sims and *Keratophora* Pantocsek, genera which also have well developed pseudocelli. Which of these resemblances are indications of affinity and which are parallelisms cannot be decided on the basis of our present knowledge.

The subocellus of *Maluina* is much smaller than that of *Solium*, *Pseudorutilaria*, and *Monile* and its areolae or porelli are much finer and more tightly and uniformly packed. These differences are so considerable as to suggest that *Maluina* may well not have any close affinity with those genera. Its elevations bear a small number of interlocking linking spines, but these are of a different shape from those in *Solium* and *Pseudorutilaria* (compare Fig. 67 with Figs 6 and 13) and it differs from those two genera in virtually every other respect. It seems to be an isolated genus and we can offer no suggestions as to its affinities.

The similarities between *Bonea* and *Strelnikovia* are such as to indicate that they are related. The many interlocking linking spines and the large pseudocellus are the characters that point to this most strongly. In *Strelnikovia antiqua* (Strel'nikova) R. Ross & P. A. Sims and *S. inclinata* R. Ross & P. A. Sims there is some sign of a vertical division of the pseudocellus at the apex of the valve (see Ross & Sims, 1985: pl. 21 fig. 5, pl. 24 fig. 6) and this is more strongly developed in *Bonea* (Fig. 73). We would therefore add *Bonea* to the group consisting of *Briggera* R. Ross & P. A. Sims, *Dicladiopsis* De Toni, *Strelnikovia* R. Ross & P. A. Sims, *Keratophora* Pantocsek, and *Thaumatonema* Greville. As we have already indicated (Ross & Sims, 1985; Sims, 1986), this group is much closer to *Biddulphia* than it is to *Hemiaulus*, and it should not be included in the Hemiauloideae. There are species of *Biddulphia* that differ from species of *Briggera* in nothing but the lack of interlocking linking spines, and other species that have all the characters of *Strelnikovia* except interlocking linking spines (see Ross & Sims, 1985: 288–290). There is the same similarity and difference between *Bonea simulans* R. Ross & P. A. Sims and *Triceratium exornatum* Greville. The significance of this for the supra-generic classification of the Biddulphiaceae remains obscure, but it does suggest that the transition between diatoms with interlocking linking spines and those without them has occurred more than once. There is, though, no real indication of the direction in which it happened.

One of us (Sims, 1986) has recently grouped together in the subfamily Hemiauloideae of the Biddulphiaceae the genera *Hemiaulus* Heiberg, *Sphynctolethus* Hanna, *Pseudaulacodiscus* Jousé, *Ailuretta* Sims, *Cerataulina* H. Peragallo, and *Eucampia* Ehrenberg. *Trinacria* Heiberg differs from *Hemiaulus* sensu stricto only in the absence of sulci or internal costae and in the number of poles and of labiate processes, and it also clearly belongs in the Hemiauloideae. Whether *Dextradonator* should also be included is more difficult to decide. It differs from *Hemiaulus* in the shape of the valve and of the linking spines, in the absence of sulci or internal costae, and in the pattern of areolation. Its very deep, coarsely areolate, entire valvocopula (Fig. 81) is another point of difference. This is a character that it shares with *Abas* R. Ross & P. A. Sims (1980), which it also resembles in shape of valve and pattern of areolation. We would for the present tentatively include both genera in the Hemiauloideae, with the proviso that they are not nearly so closely related to the rest of the subfamily as the other genera included in it are to one another.

Our main conclusion must be, then, that the information presented here makes the supra-generic classification of the genera that have been included in the Biddulphiaceae and the so-called Eupodiscaceae more difficult rather than less. That this is so is probably to be attributed to the fact that our knowledge of the Cretaceous and Paleogene diatom floras is still inadequate, and will perhaps always be so.

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Description of plates

Plates 1–11 are SEM micrographs.

Plates 12–13 are LM micrographs.

Plate 1. *Solium exsculptum* Heiberg. Figs 1–3, 5, 6: forma *exsculptum*, 'Kamischev', presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.; Fig. 4: forma *pentagona* Jousé, Northern Urals, Tyumen'sk oblast, U.S.S.R.; Figs 1, 3, 4: bar line = 10 μm; Figs 2, 5, 6: bar line = 2 μm.

Fig. 1: valve exterior tilted and displaying four projections with elevations separated from central domed area by deep sulci, well-developed marginal ridge (arrowhead), numerous hollow spines (or occluded

processes), and single labiate process (arrow). Fig. 2: same specimen, detail of distal side of elevation with subocellus of areolae in radial rows positioned on upper part of elevation, linking spines, and concave mantle. Note also costae on mantle and elevation. Fig. 3: oblique view of frustule linked to single valve; fragments of girdle bands present. Fig. 4: oblique view of valve exterior of 5-polar form with concave mantle, sulci separating projections from central portion which has irregularly scattered areolae and an off-centre single labiate process. Fig. 5: distal side of linked elevations with clearly-defined subocelli apposed and single rows of poroid areolae between anastomosing costae. Note each areola is bordered by a rim with a single small spine and occluded by a vola. Fig. 6: proximal face of tips of two elevations linked by expanded and interlocking linking spines.

Plate 2. *Pseudorutilaria monile* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni, Division Hill, Otago, New Zealand. Figs 7–9, 11: bar line = 20 μm; Figs 10, 12, 13, 14: bar line = 3 μm.

Fig. 7: girdle view of two valves linked at elevations. Note central circular domed area, also regular rows of spines arising from marginal ridge between central portion and each elevation. Figs 8, 9: valve exterior with almost circular central portion and projections with crenulate margins gently tapering from central portion to each pole. Fig. 10: central portion with entire margin, sparse and scattered poroid areolae, irregular ring of troughs with raised margins (one broken occluded process (arrow) clasped within trough) mostly alternating with the fractured occluded processes (arrowhead). Fig. 11: two linked valves, oblique view of valve interior showing transapical costae positioned at each indentation of the valve margin. Fig. 12: valve interior with opening from single labiate process. Fig. 13: interlocking linking spines at tips of linked elevations on proximal sides. Fig. 14: oblique view of two linked elevations with a subocellus positioned just beneath each tip, linking spines on the proximal faces and solid spines arising from marginal ridge.

Plate 3. *Pseudorutilaria clavata* R. Ross & P. A. Sims. Figs 15, 16, 18–23: south-western Atlantic, Falkland Plateau, 51° 08′S, 54° 22′ W, 1525 m depth, Vema cruise 17, core 107, 50 cm. Fig. 17: south-western Atlantic, Falkland Plateau, 53° 01′ S, 52° 52′ W, 2880 m depth, Vema cruise 18, core 104, 330 cm. Figs 15–17, 19, 20: bar line = 20 μm; Figs 18, 21–23: bar line = 5 μm.

Figs 15–17: exterior views showing valve outline with almost circular central portion, gibbous portion on either side with each projection tapering to clavate rounded apices. Note marginal spines on marginal ridge and undulate valve face. Fig. 18: girdle view, two linked valves at centre, each with occluded processes and single labiate process (arrow) clasped within troughs with raised margins (two arrows) of opposing valve. Note girdle band with finely poroid areolae. Figs 19, 20: valve interior with four transverse sulci visible, positioned between central portion, gibbous portions, and projections. Note valve margin is entire, also note opening from single labiate process on fig. 20. Fig. 21: central portion with ring of occluded processes (broken at base), base of labiate process (arrow), also troughs with raised margins, one enclosing process of sibling valve. Fig. 22: distal side of low elevation with subocellus and four linking spines, one broken at base. Fig. 23: girdle view showing interlocking linking spines at tips of proximal faces of low elevations, apposed subocelli clearly defined, also flattened spines arising from marginal ridge. Note also deep furrow between mantle and hyaline marginal band, also anastomosing costae.

Plate 4. *Pseudorutilaria nodosa* R. Ross & P. A. Sims.

Figs 24–27, 29, 32: 'Lamont E8'; Figs 28, 33: south-western Atlantic, Falkland Plateau, 53° 01′ S, 52° 52′ W, 2880 m depth, Vema cruise 18, core 104, 330 cm. Figs 24–28, bar line = 20 μm; Figs 29–33, bar line = 5 μm.

Fig. 24: oblique view of two linked valves showing valve interior with numerous transverse costae. Fig. 25: oblique view of valve exterior showing undulate valve face, domed central portion, distinct marginal ridge and vertical mantle with deep furrow above narrow marginal band. Figs 26, 27: same specimens lying flat, displaying distinctive valve outline. Fig. 28: specimen with straight, not curved valves. Note position of gibbous portions and arrangement of internal costae identical with those above. Fig. 29: central portion, exterior view, with ring of fractured occluded processes alternating with troughs with fractured margins, also scattered poroid areolae. Fig. 30: linked elevations with subocelli on distal side and linking spines on proximal face, also long solid spines arising from marginal ridge. Fig. 31: single elevation with eroded linking spines. Fig. 32: two linked valves, central portion, with external openings from two labiate processes visible (arrows), one from each valve inclined and lying on opposing valve margin. Note also raised margins of troughs and indentation at base of mantle. Fig. 33: interior view, central portion, showing opening from single labiate process and transapical costae.

Plate 5. *Pseudorutilaria hannai* R. Ross & P. A. Sims. South-western Atlantic, Falkland Plateau, 53° 01′ S, 52° 52′ W, 2880 m depth; Vema cruise 18, core 104, 330 cm. All figures are of the same specimen. Figs 34, 35: bar line = 30 μm; Figs 36–38: bar line = 5 μm.

Fig. 34: two linked valves, interior view with central circular portion defined by transverse costae and curved projections regularly crossed by costae. Fig. 35: specimen in almost girdle view showing undulate margin and spines from marginal ridge of both valves alternating along complete length of valve. Fig. 36:

view at pole with interlocking linking spines on proximal face of each low elevation, subocellus missing on distal side and indentation or deep furrow between concave mantle and marginal hyaline band. Fig. 37: exterior opening of labiate process from upper valve (arrow) positioned between marginal spines. Fig. 38: central portion with slit-like opening from single labiate process (arrow). Note also scattered areolae and furrow between mantle and valve margin in central portion.

Plate 6. *Pseudorutilaria incompleta* R. Ross & P. A. Sims.

Figs 39–46: south-western Atlantic, Falkland Plateau, 51° 08′ S, 54° 22′ W, 1525 m depth, Vema cruise 17, core 107. Fig. 47: south-western Atlantic, Falkland Plateau, 47° 45·7′ S, 57° 38·5′ W, 3650 m depth, Conrad cruise 12, core 237. Figs 39–41: bar line = 20 μm; Figs 42–44: bar line = 2 μm; Figs 45–47: bar line = 5 μm.

Figs 39, 40: valve exterior of separation valve and valve within chain displaying distinctive valve outline with crenulate margin, sulci producing undulate valve surface and the pentagonal central portion. Fig. 41: two linked valves tilted to show valve interior with sulci positioned between each crenulation and a large pentagonal central portion. Fig. 42: separation valve at pole with subocellus positioned just beneath tip of low elevation and single large spine on proximal margin. Fig. 43: distal side of linked elevations with discrete subocellus beneath tip of each elevation. Fig. 44: girdle view of same specimen with discrete subocelli and interlocking linking spines, areolae with vela, also marginal spines interdigitating. Fig. 45: central portion of separation valve with single straight labiate process, hyaline circular area surrounded by low flange-like costa, also scattered poroid areolae. Fig. 46: central portion, valve exterior with base of single labiate process (arrow), occluded processes and eroded troughs with raised margins arranged in circle. Fig. 47: central portion, valve interior, with opening from single labiate process, crenulate margin and internal sulci.

Plate 7. *Pseudorutilaria hendeyi* R. Ross & P. A. Sims.

Figs 48, 49, 53: south-western Atlantic, Falkland Plateau, 53° 01′S, 52° 52′ W, 2880 m depth, Vema cruise 18, core 104, 330 cm. Figs 50–52, 54: south-western Atlantic, Falkland Plateau, 51° 08′ S, 54° 22′ W, 1525 m depth, Vema cruise 17, core 107, 50 cm. Figs 48, 50: bar line = 20 μm; Figs 49, 51–54: bar line = 5 μm.

Fig. 48: oblique view of triangular valve with central area defined by three sulci, long projections with undulate surface and rounded apices. Fig. 49: central portion fractured at centre but surrounded by remains of occluded processes, labiate processes and troughs. Fig. 50: interior view, two linked valves with transverse sulci proximally and costae distally across each projection and crenulate valve margin. Fig. 51: interior view, central portion, with openings from two labiate processes, scattered poroid areolae and patch of porelli. Fig. 52: fractured specimen, two linked valves, view looking into valve centre with occluded processes (arrow) and troughs with raised margins (arrowheads). Note marginal spines interdigitating. Fig. 53: single projection with low elevation. Exterior view showing position of linking spines on proximal face. Fig. 54: two linked valves, polar view of projection with low elevations, remains of well-defined subocelli and internal costae on upper valve.

Plate 8. *Monile laurentii* R. Ross & P. A. Sims. St. Laurent-la-Vernède, Gard, France. Figs 55–60: bar line = 25 μm; Figs 61–64: bar line = 5 μm.

Figs 55, 56: single valves, exterior view, showing sinuous valve outline, domed central portion, sub-clavate apices and elevations with flattened summits. Fig. 57: oblique view, valve exterior, with vertical mantle on which there are three central and a polar indentation. Figs 58–59: interior view, single valves with transapical sulci positioned at each indentation of valve margin. Fig. 60: frustule with attached girdle band. Upper valve with undulate valve face, openings from four labiate processes on central portion and flattened summits to short, squat elevations. Fig. 61: central portion with exterior openings from four labiate processes projecting as fractured hollow spines, poroid areolae each with slightly raised rim with one or two small solid spines and occluded by cribrum. Fig. 62: interior view, central portion, with openings from four labiate processes. Fig. 63: proximal face of elevation with flattened summit encircled by marginal row of low teeth, areolae with cribra and interstrial pores. Fig. 64: distal side of elevation, expanded above, flattened summit bearing ring of low radial teeth on margin and subocellus on summit and expanded tip. Note anastomosing costae on elevation.

Plate 9. *Maluina centralitenuis* (R. Ross & P. A. Sims) R. Ross & P. A. Sims. Figs 65–70: south-western Atlantic, Falkland Plateau, 51° 08′ S, 54° 22′ W, 1525 m depth, Vema cruise 17, core 107, 50 cm. Fig. 65: bar line = 20 μm; Figs 66–70; bar line = 5 μm.

Fig. 65: two linked valves with cylindrical elevations, vertical mantles with strongly developed pseudo-antiligulae at apices and domed centres. Fig. 66: detail of mantle with single row of poroid areolae and pseudo-antiligula, central domed area with radial rows of poroid areolae and single labiate process. Fig. 67: proximal face of cylindrical elevations with linking spines, expanded above and interlocking. Fig. 68: distal side of elevations, each with small subocellus at its tip. Note scattered areolae. Fig. 69: valve interior with large, slit-like opening from single labiate process, rows of fine areolae radiating from valve centre to margin of dome, also on outer valve face but sparse on vertical mantle. Fig. 70: valve exterior with small

circular hyaline central area, rows of fine poroid areolae radiating to base of domed centre, also opening from single labiate process projecting as a small tubular spine.

Plate 10. *Bonea simulans* R. Ross & P. A. Sims. 'Carlovo', U.S.S.R. Figs 71, 72, 74: bar line = 20 μm; Figs 73, 75–77: bar line = 3 μm.

Fig. 71: valve exterior, triangular valve with low elevations with flattened summits, marginal ridge between elevations bearing large spines, also vertical mantle. Fig. 72: valve interior showing weakly folded valve face with opening from single central labiate process. Fig. 73: elevation with summit surrounded by complete ring of expanded solid spines, those on the distal margin fractured. Note pseudocellus on summit and tip of elevation. Fig. 74: girdle view of frustule linked to two valves with two girdle bands present. Note pseudocellus on distal side of each elevation, also the interdigitating marginal spines. Fig. 75: distal side of elevations linked by numerous small expanded spines which interlock with those of the apposing elevation. Fig. 76: poroid areolae occluded by rotae with *c.* nine spokes, also single interstrial pore. Fig. 77: occlusion to smaller poroid areolae, also two interstrial pores.

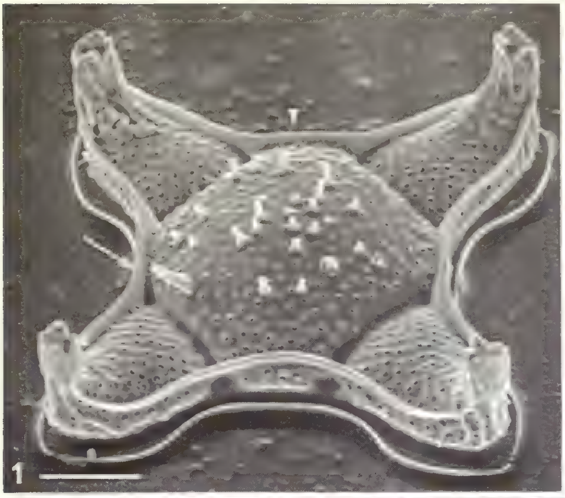
Plate 11. *Dextradonator eximius* (Grunow) R. Ross & P. A. Sims. Indian Ocean, 10° 25′ S, 63° 15′ E, 3115 m depth, dredge sample DODO-123-D1. Figs 78–83: bar line = 20 μm; Figs 84–85: bar line = 10 μm. Identity of specimen shown in Figs 82–3 doubtful (see p. 289).

Fig. 78: two valves linked, upper with hyaline band (pleura) attached. Note linking mechanism involving two flattened and acute linking spines partially encircling elevation of sibling valve. Fig. 79: oblique view, same specimen, with hyaline marginal ridge turned inwards between elevations (arrows). Fig. 80: linked circular valves with broad vertical mantles, upper with attached valvocopula, lower with hyaline mantle and marginal ridge turned inwards. Fig. 81: single valve with attached valvocopula, cylindrical elevations each with two fractured linking spines. Fig. 82: linked valves, girdle view. Note two spines from each valve projecting beyond the girdle bands. Fig. 83: oblique view, valve face with small hyaline central area, radiating rows of fine poroid areolae extending to marginal ridge and slightly beyond base of elevations, also two long spines arising from marginal ridge. Fig. 84: distal side of elevation with few scattered areolae at tip, also circular valve face with marginal ridge turned inwards. Fig. 85: valve interior, showing central hyaline area, rows of fine poroid areolae radiating from centre, also broad valve margin.

Plate 12. Figs 86–88: *Solium exsculptum* Heiberg. 'Kamischev' presumed to be Kamyshlov, Sverdlovsk oblast, U.S.S.R.

Fig. 86: fo. *exsculptum* BM 81304: frustule with valves linked on either side, girdle view, 86·5 × 32 μm. Fig. 87: fo. *pentagona* Jousé, BM 65833: 36 μm diameter. Fig. 88: fo. *exsculptum* BM coll. Adams TS748: full length one side, 67 μm. Fig. 89: *Pseudorutilaria monile* (Grove & Sturt ex De Toni & Levi) Grove & Sturt ex De Toni, BM 63397: Oamaru, New Zealand: length of specimens a: 136 μm, b: 97 μm, c: 130 μm. Figs 90, 91: *Pseudorutilaria clavata* R. Ross & P. A. Sims, BM 81136: south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107, 175 cm; Fig. 90: girdle view, two linked valves; apical axis 156 μm; Fig. 91: Holotype; apical axis 95 μm. Fig. 92: *Pseudorutilaria nodosa* R. Ross & P. A. Sims, Holotype, BM 81138: south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107, 50 cm; apical axis 146 μm. Fig. 93: *Pseudorutilaria hannai* R. Ross & P. A. Sims, Holotype, BM 81300: south-western Atlantic, 53° 01′ S, 52° 52′ W, 2880 m depth; Vema cruise 18, core 104, 330 cm; apical axis 152 μm.

Plate 13. Figs 94–95: *Pseudorutilaria incompleta* R. Ross & P. A. Sims, BM 81139: south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107. Fig. 94: Holotype; apical axis 98 μm. Fig. 95: two linked valves; apical axis 80 μm. Fig. 96: *Pseudorutilaria hendeyi* R. Ross & P. A. Sims, Holotype; BM 81142: south-western Atlantic, 51° 08′ S, 54° 22′ W, 1525 m depth; Vema cruise 17, core 107, 170 cm; apex to apex = 180 μm. Figs 97–98: *Monile laurentii* R. Ross & P. A. Sims, St Laurent-la-Vernède, Gard, France. Fig. 97: Holotype, BM coll. Adams H941, specim. I, 12: apical axis 220 μm. Fig. 98: BM 81303: apical axis 228 μm. Figs 99–100: *Bonea simulans* R. Ross & P. A. Sims. 'Carlovo', U.S.S.R.; Fig. 99: Holotype, BM 81301: length of side 119 μm. Fig. 100: BM 81302: girdle view; length of side 140 μm.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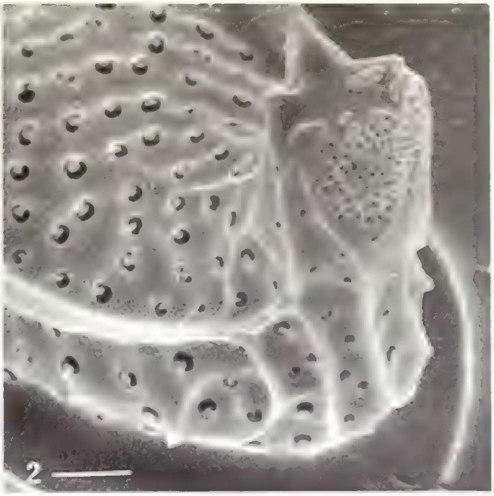
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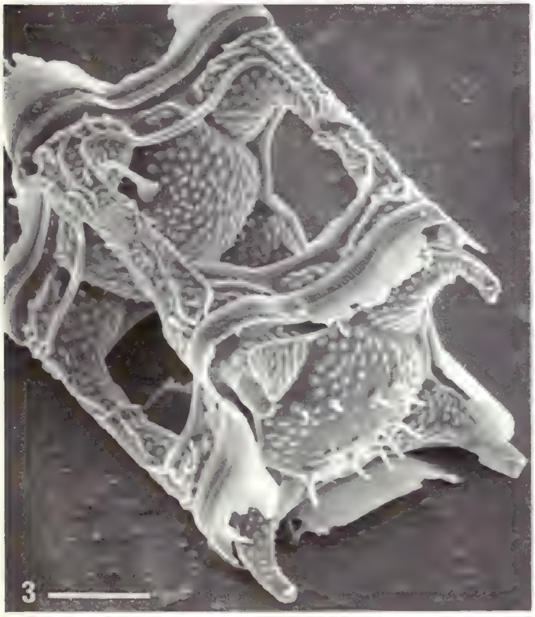
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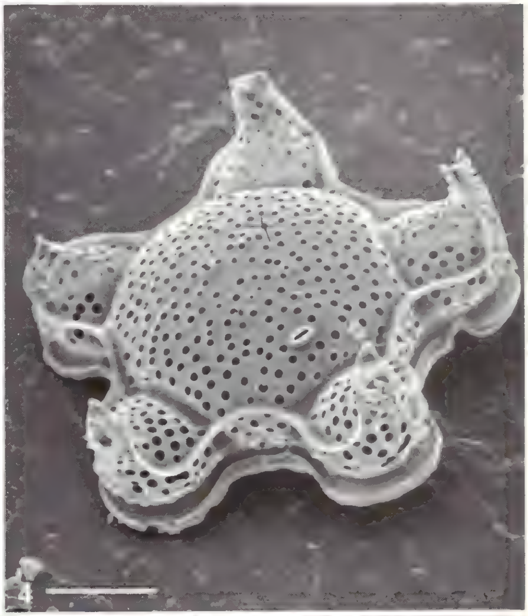
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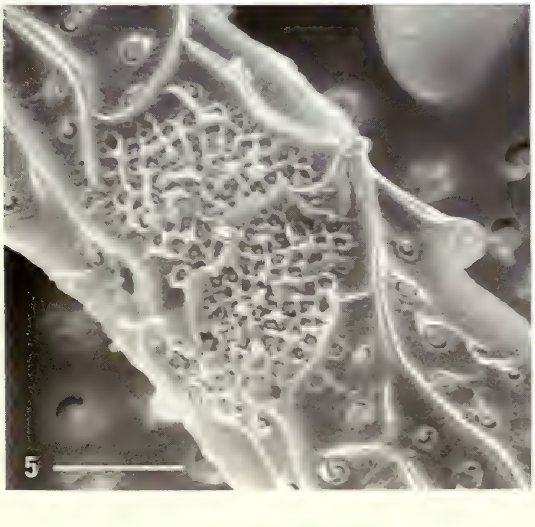
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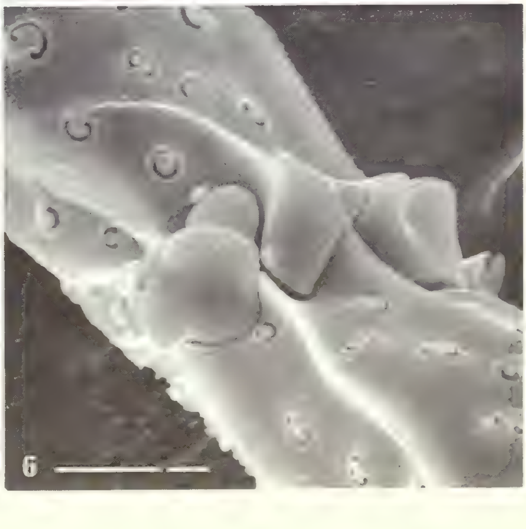
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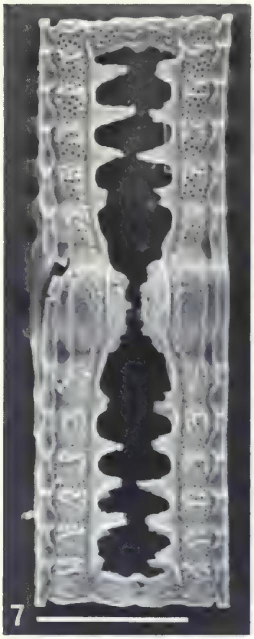
PLATE 2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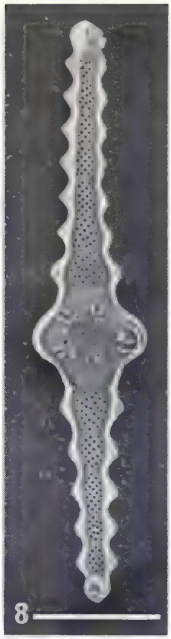
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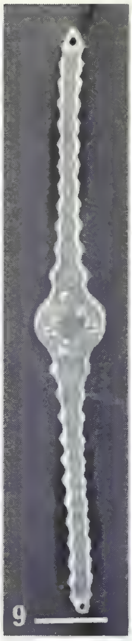
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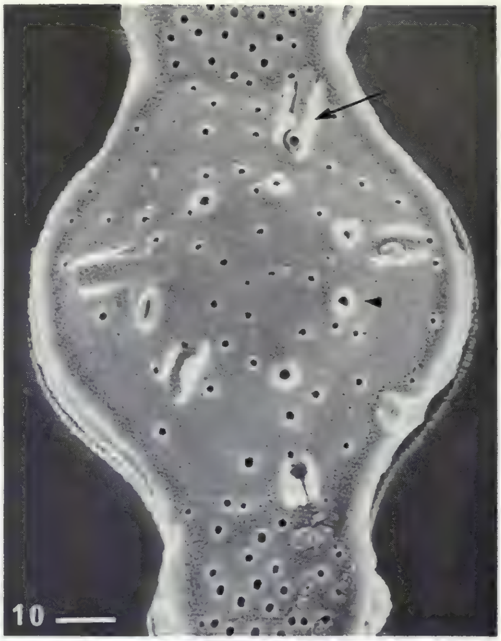
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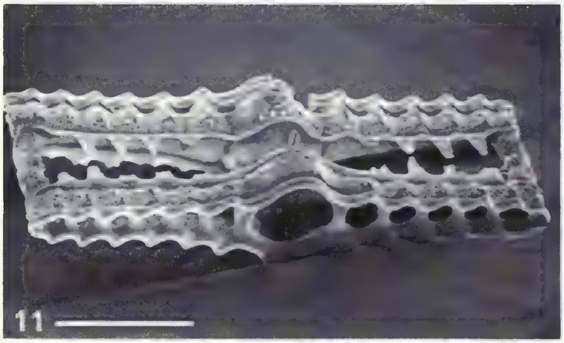
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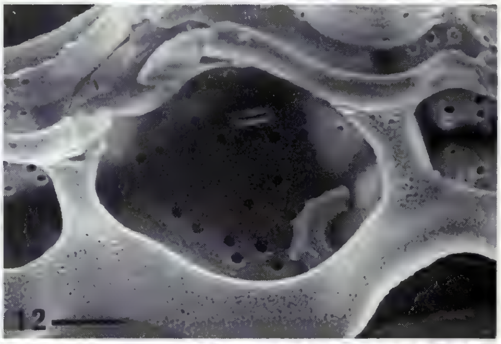
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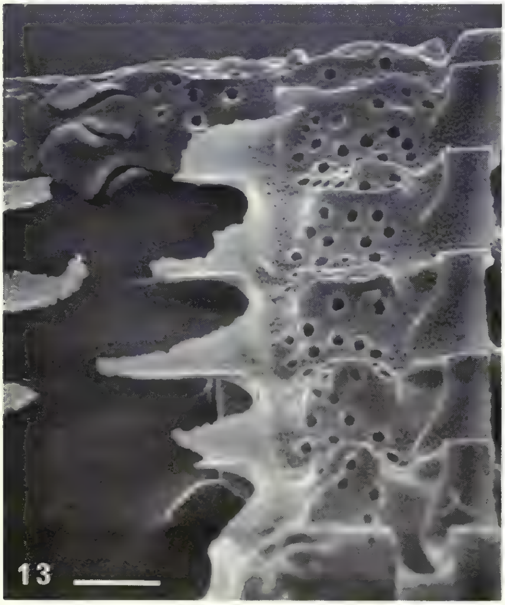
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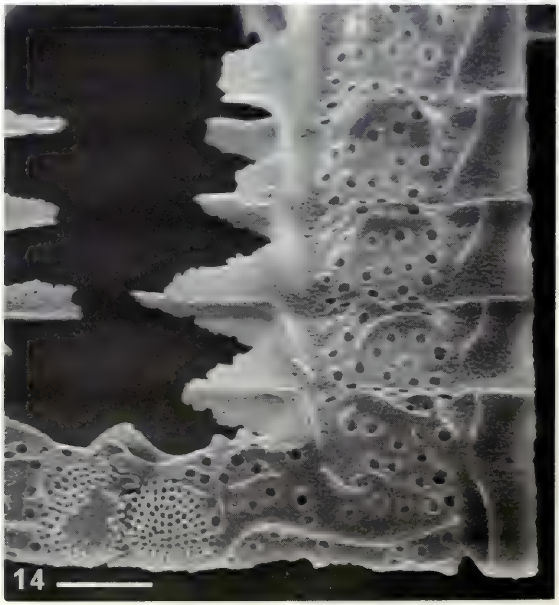
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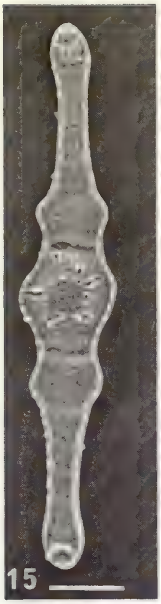
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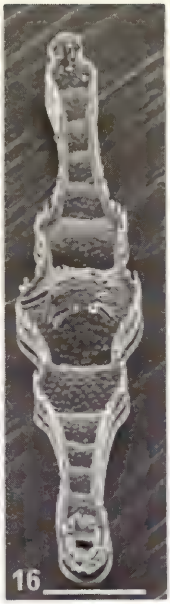
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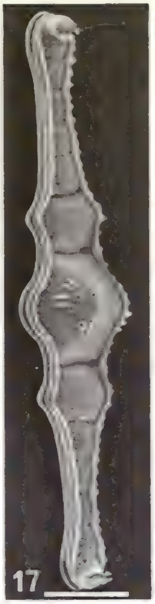
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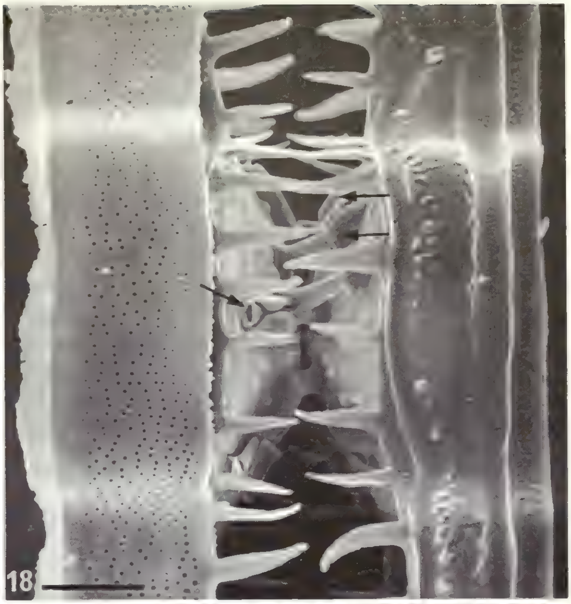
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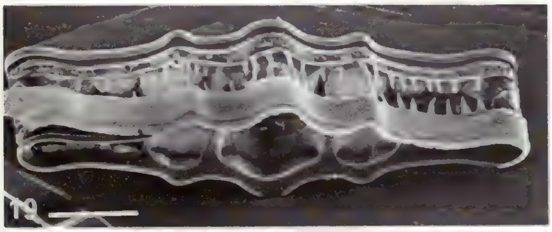
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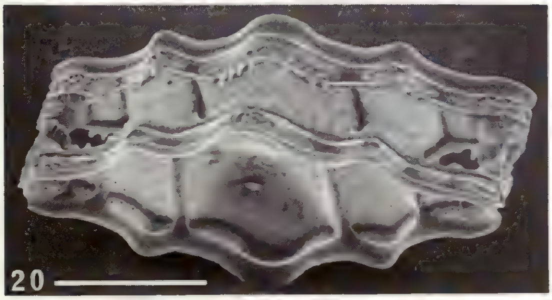
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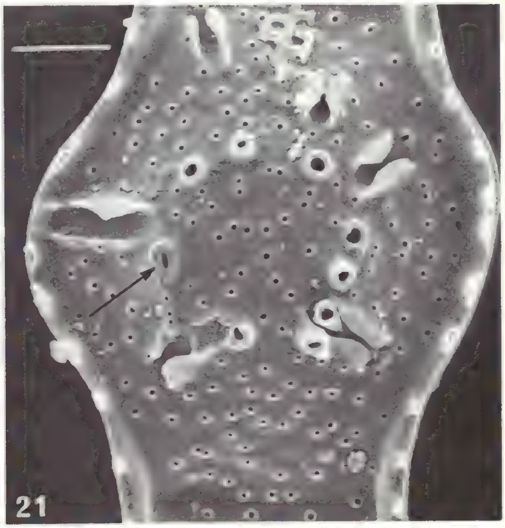
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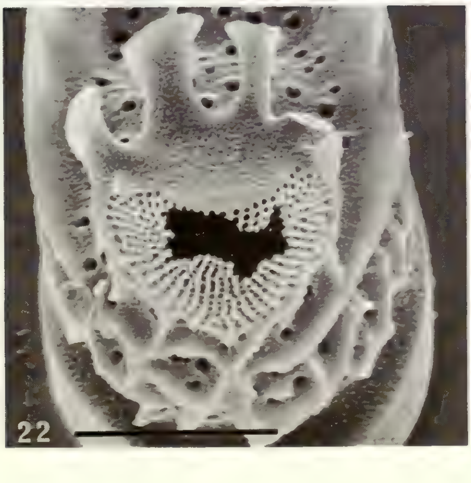
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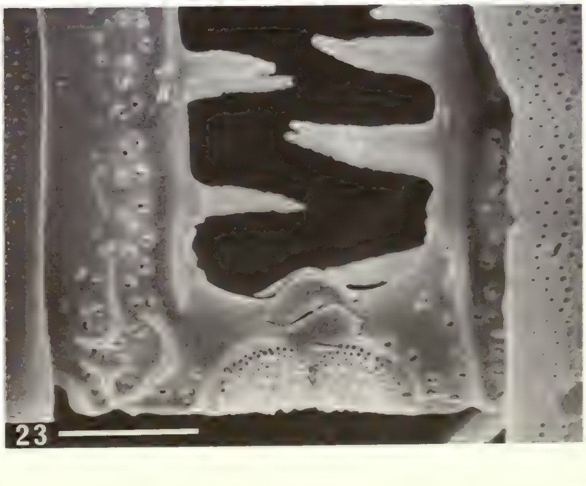
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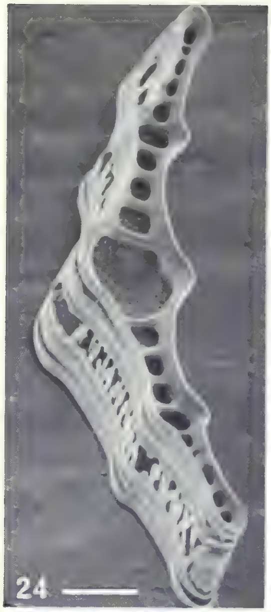
PLATE 4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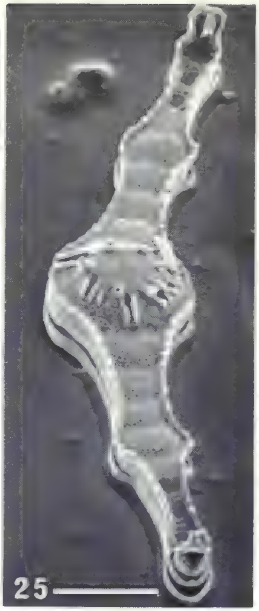
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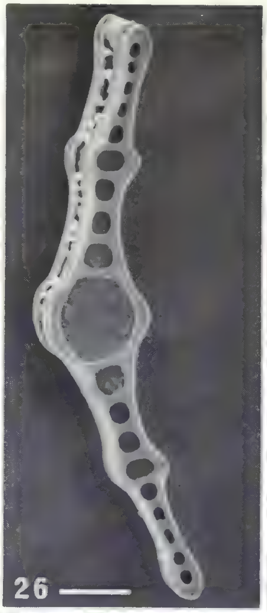
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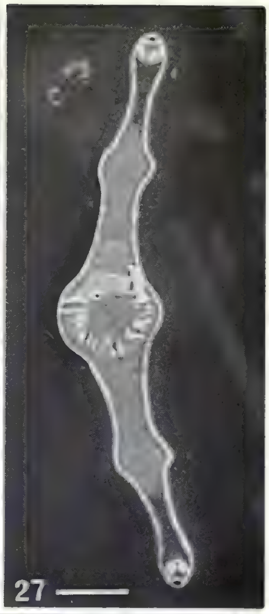
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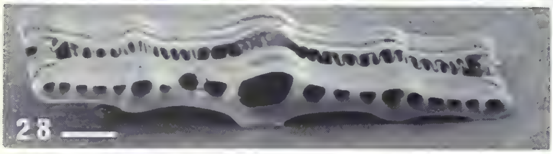
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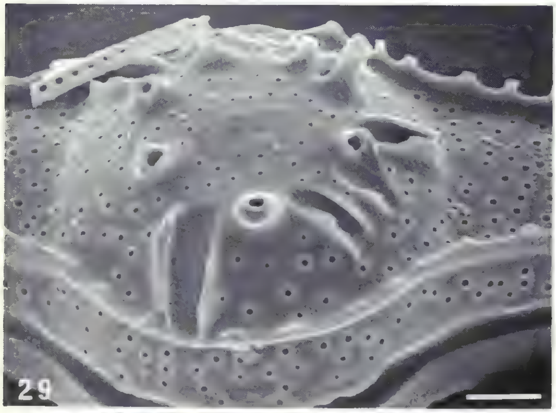
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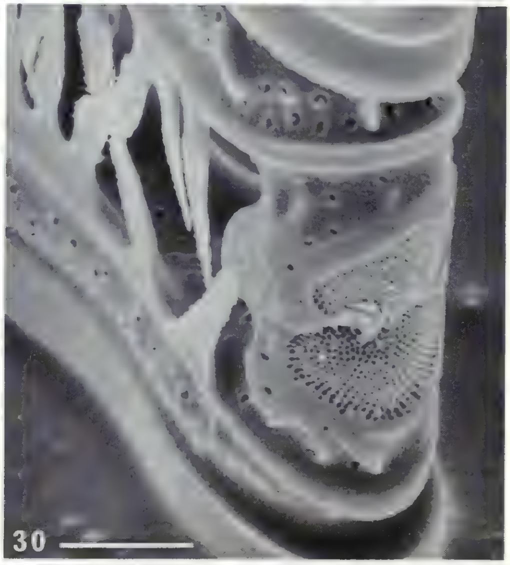
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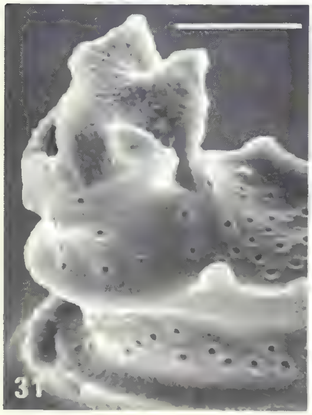
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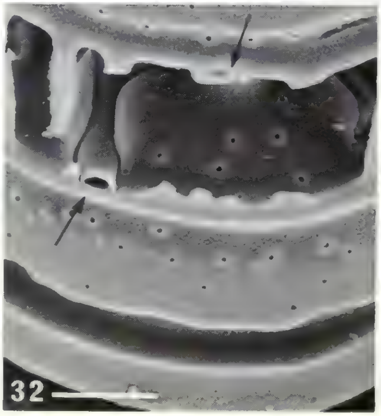
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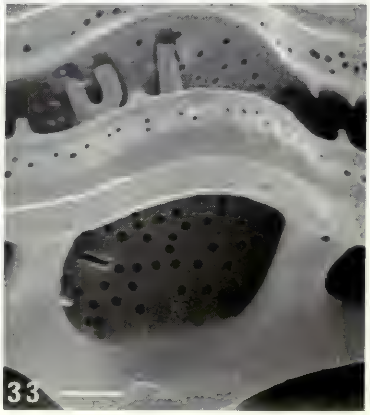
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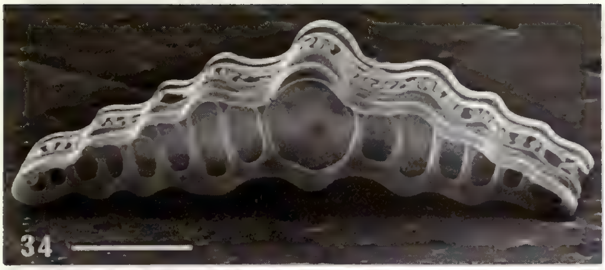
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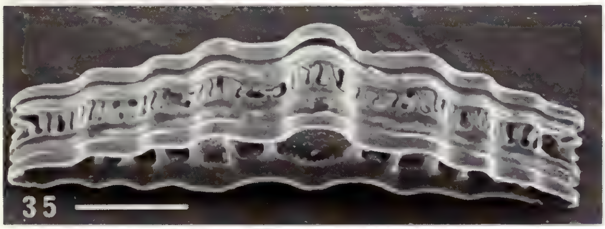
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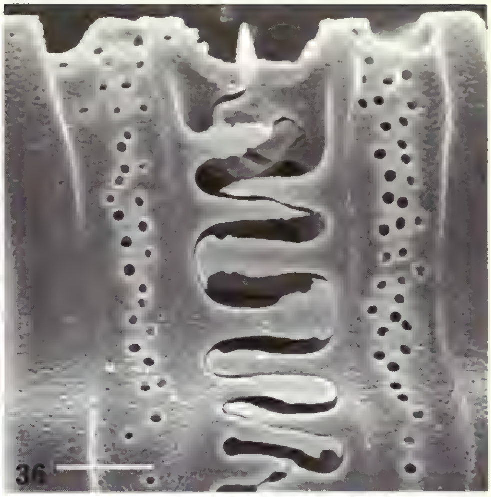
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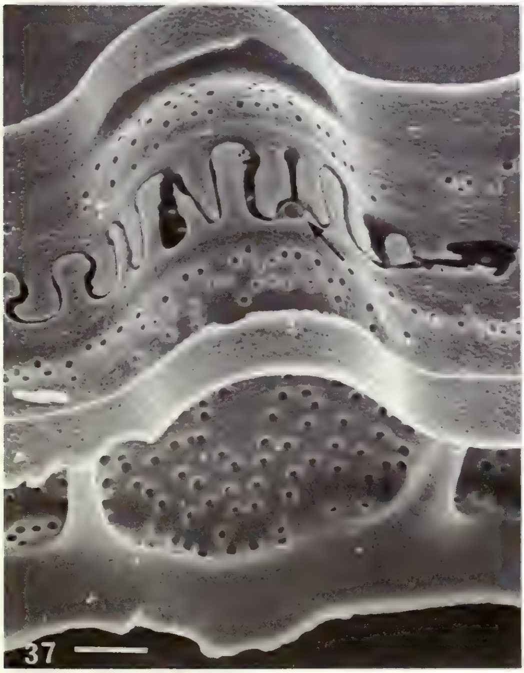
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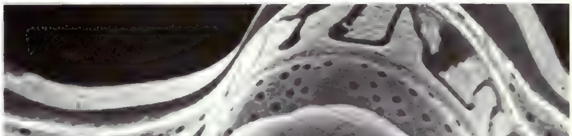
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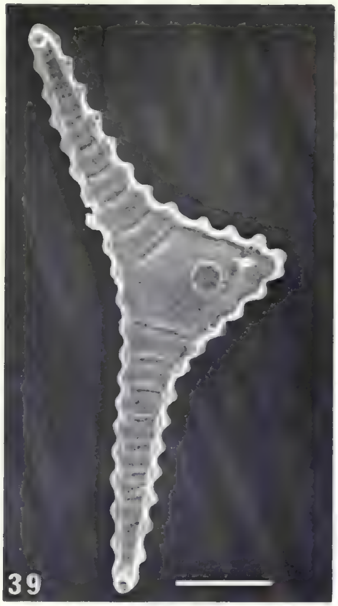
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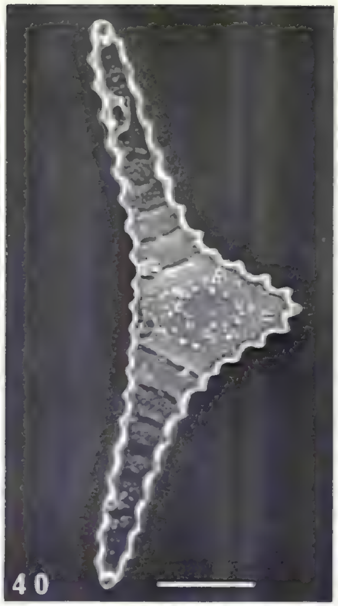
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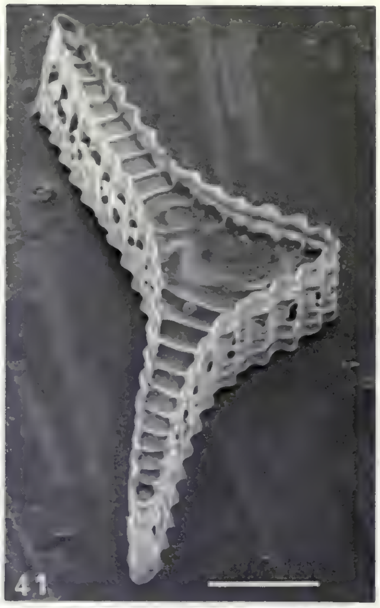
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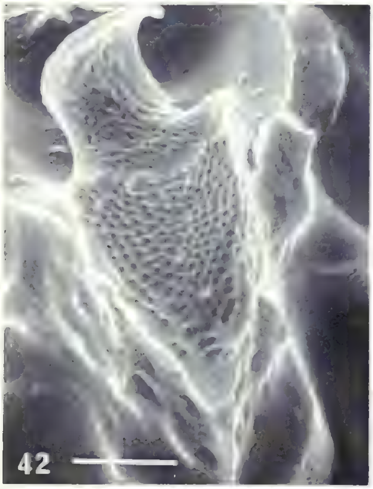
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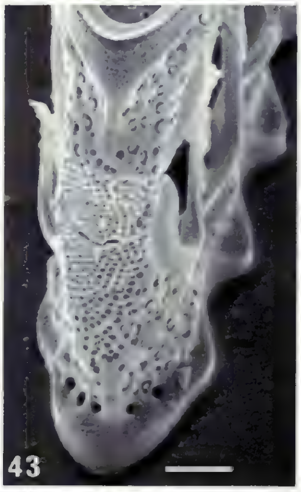
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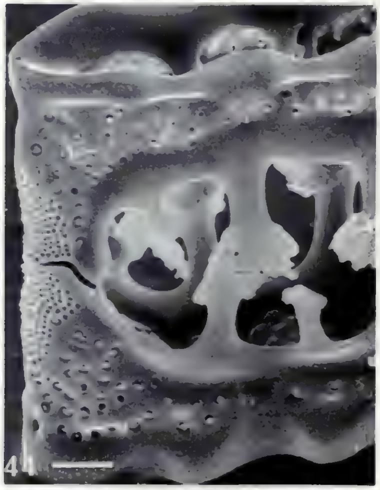
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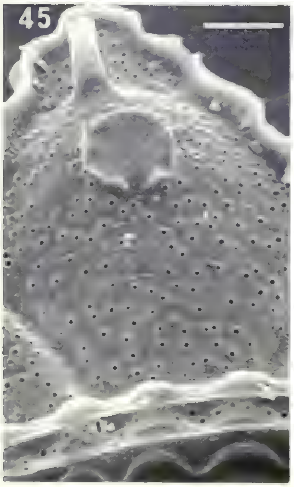
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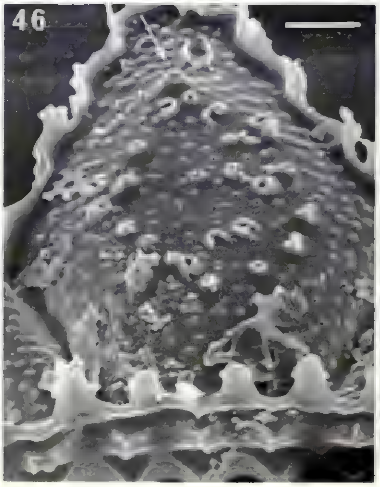
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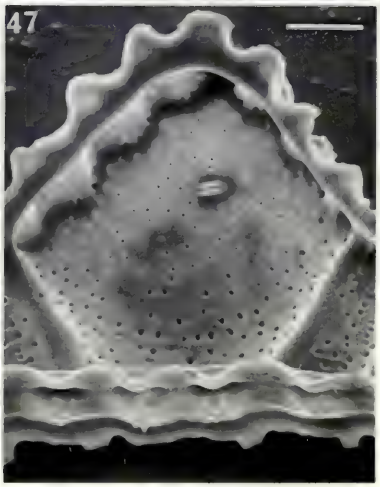
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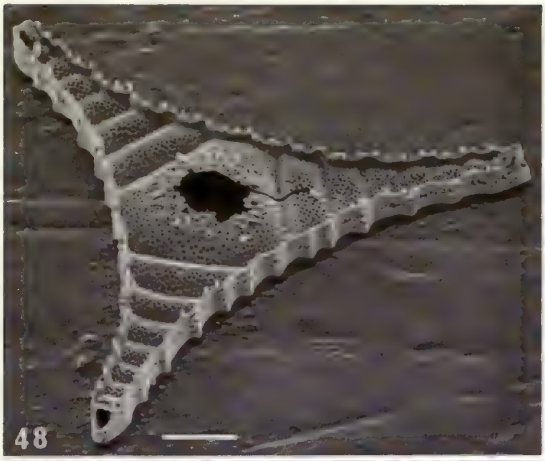
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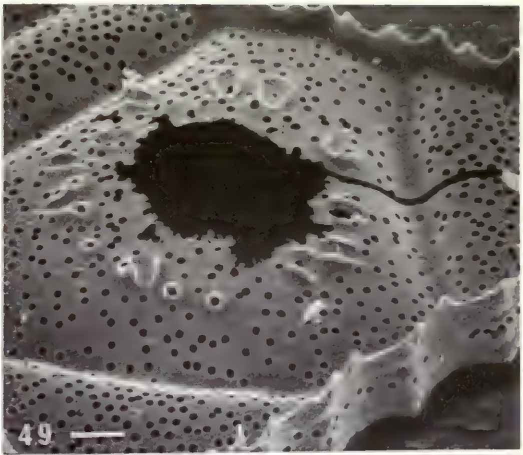
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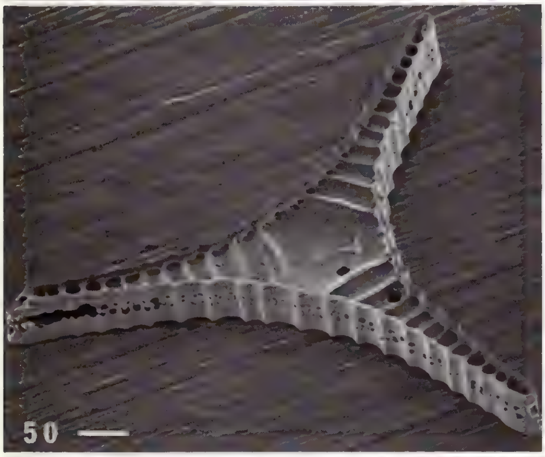
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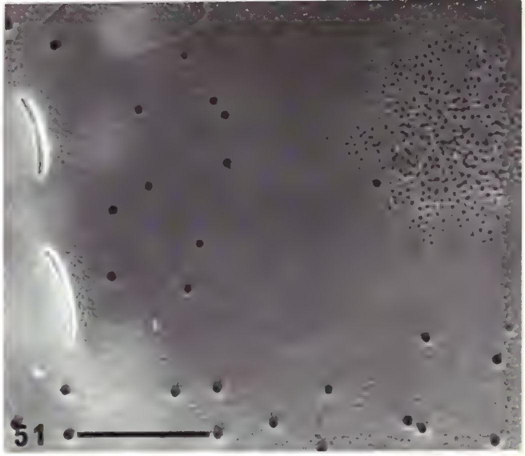
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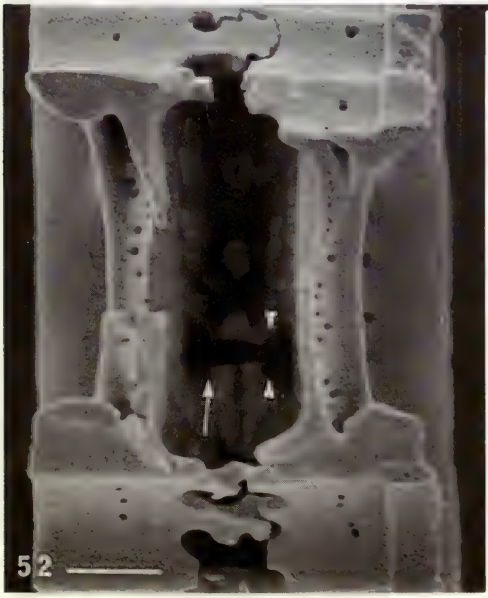
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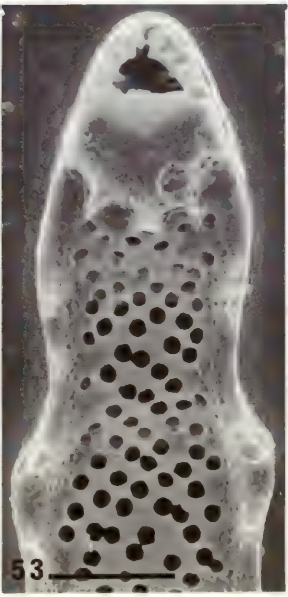
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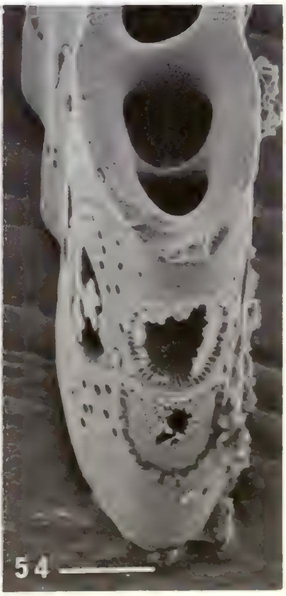
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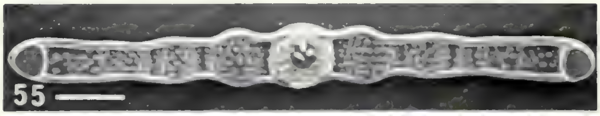
PLATE 8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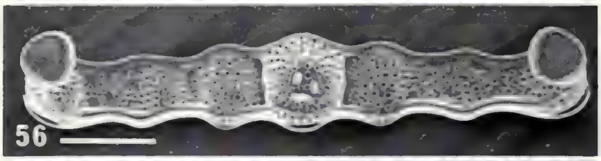
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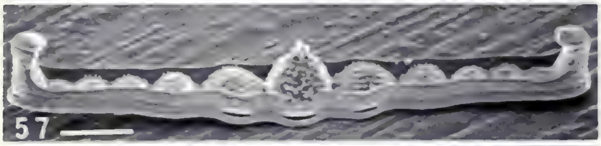
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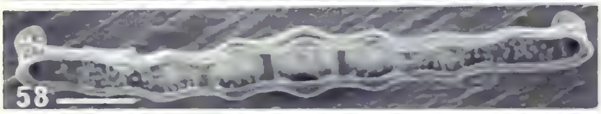
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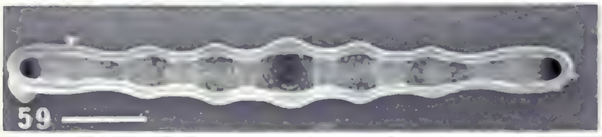
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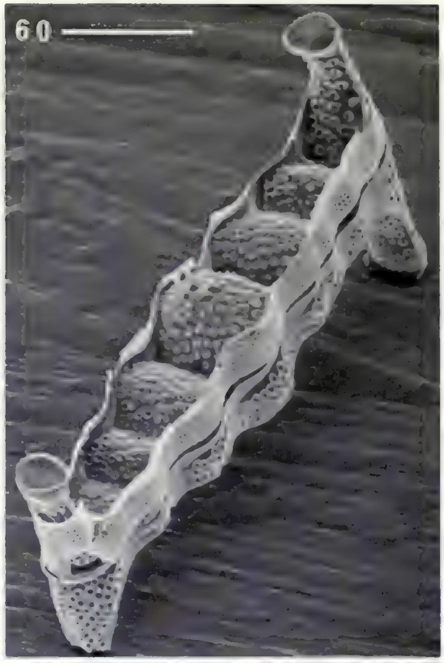
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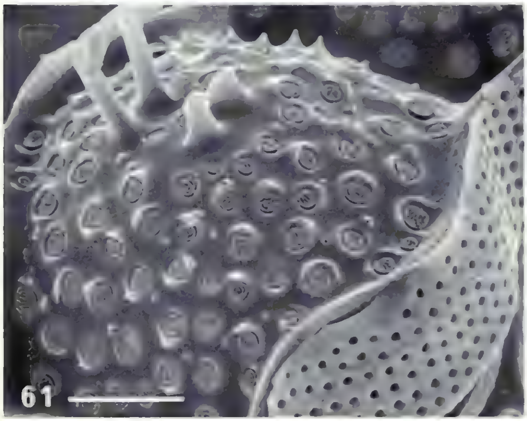
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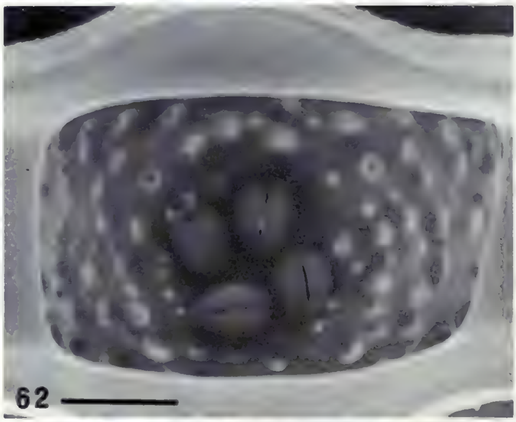
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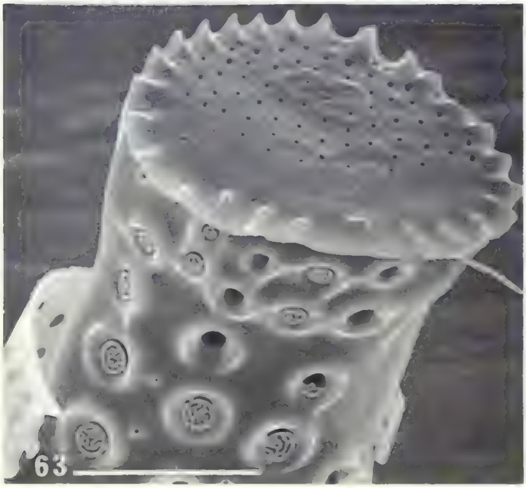
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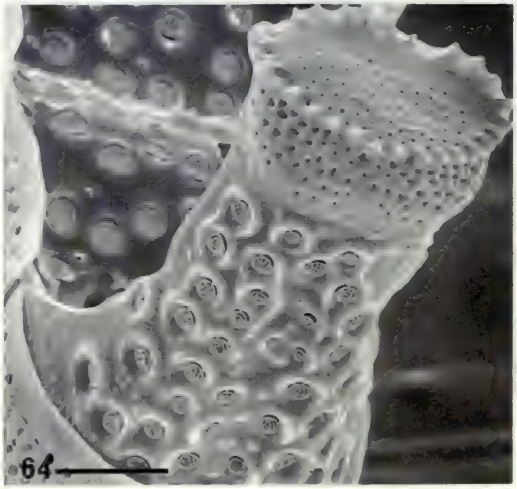
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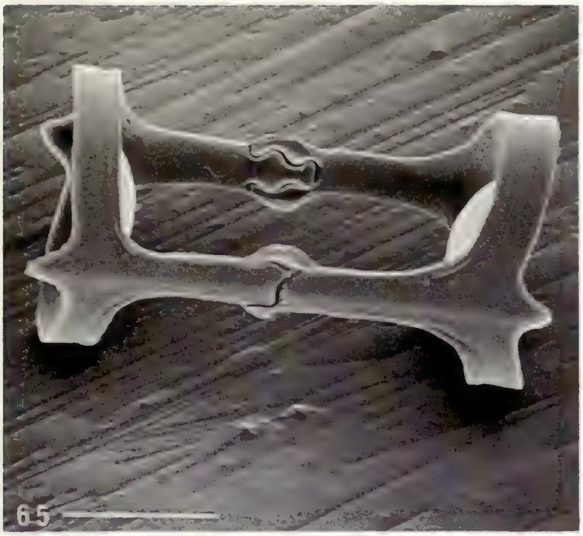
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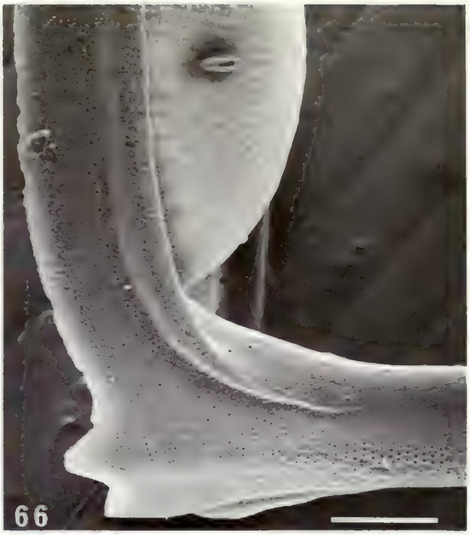
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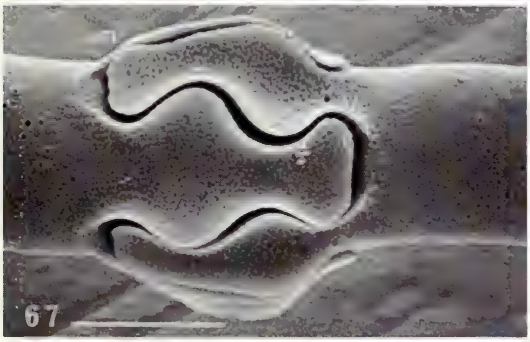
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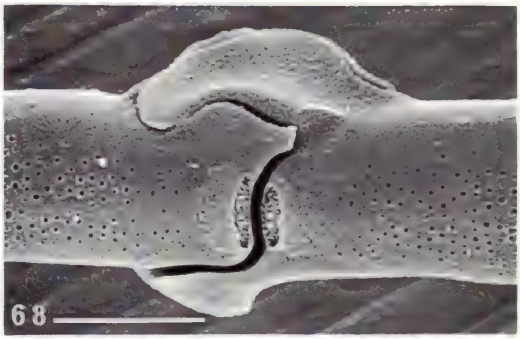
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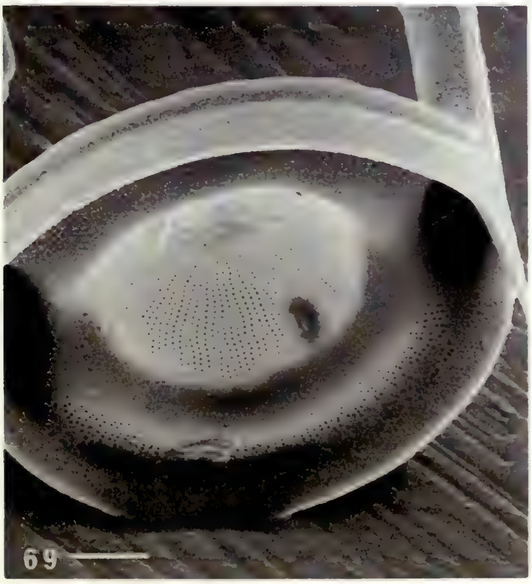
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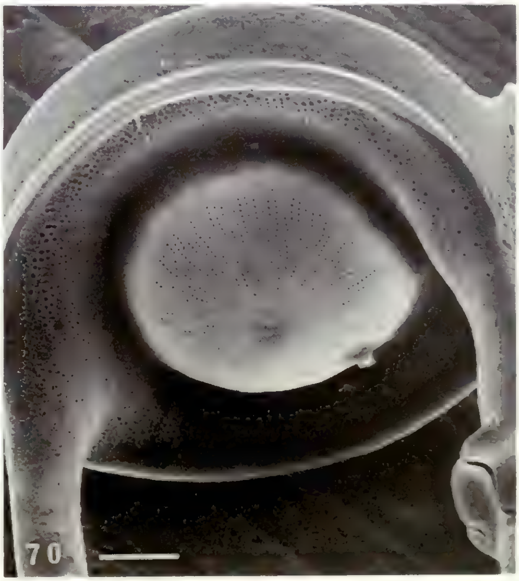
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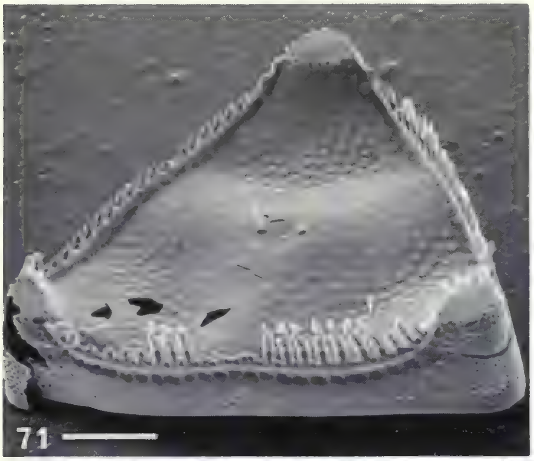
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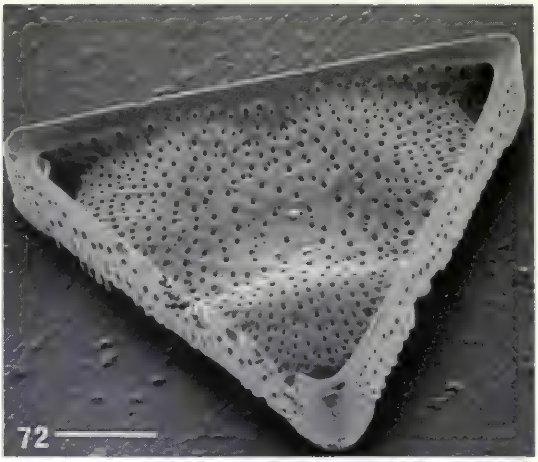
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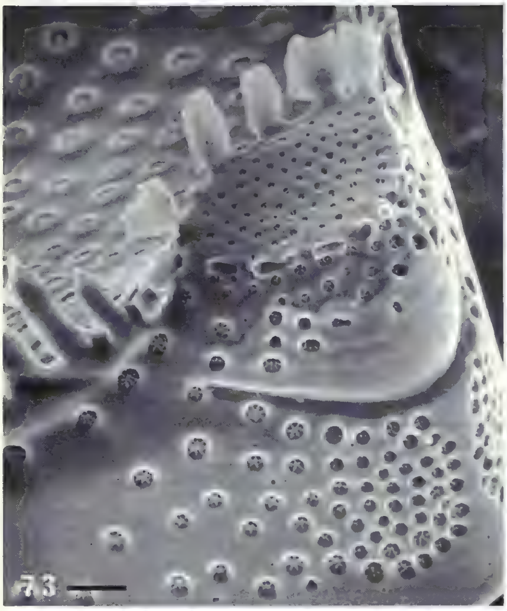
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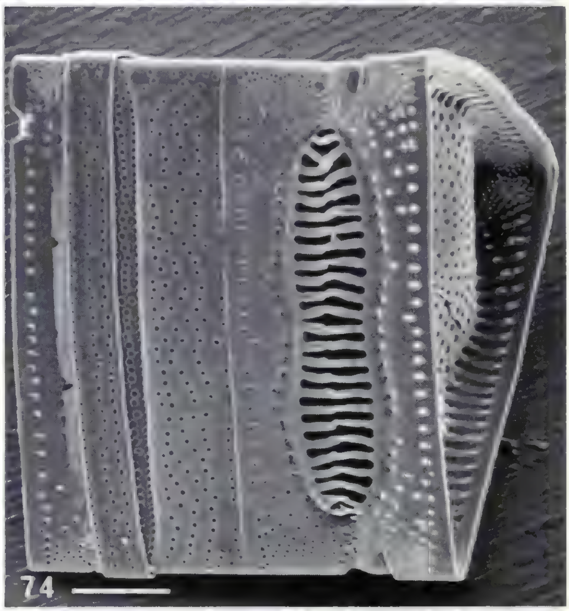
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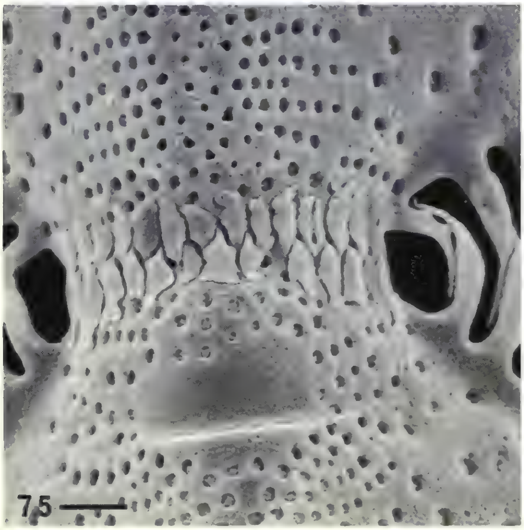
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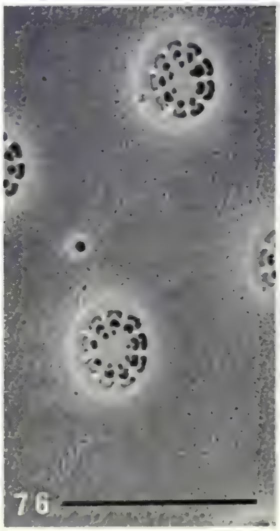
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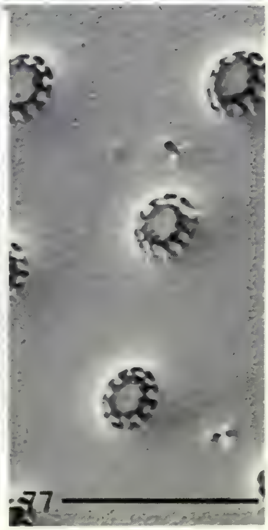
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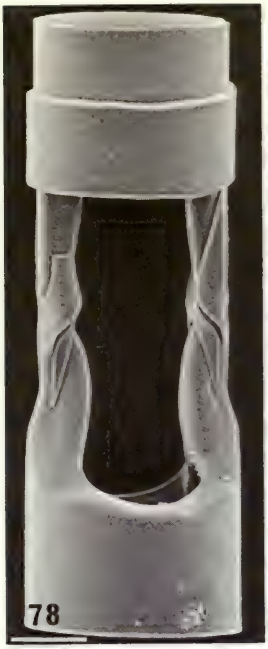
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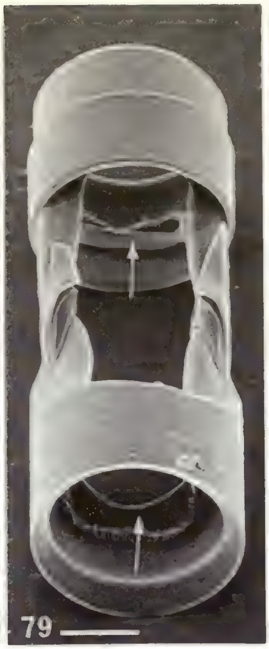
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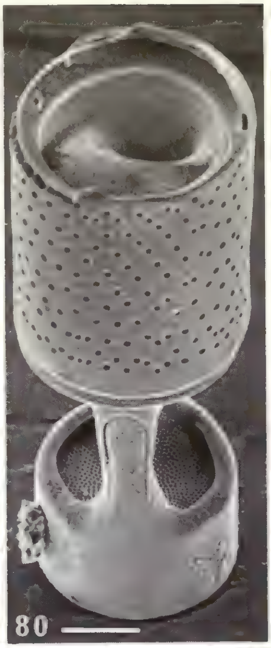
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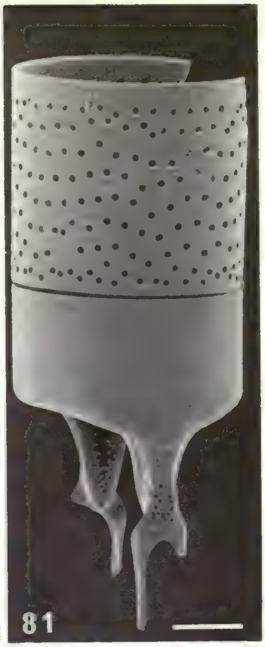
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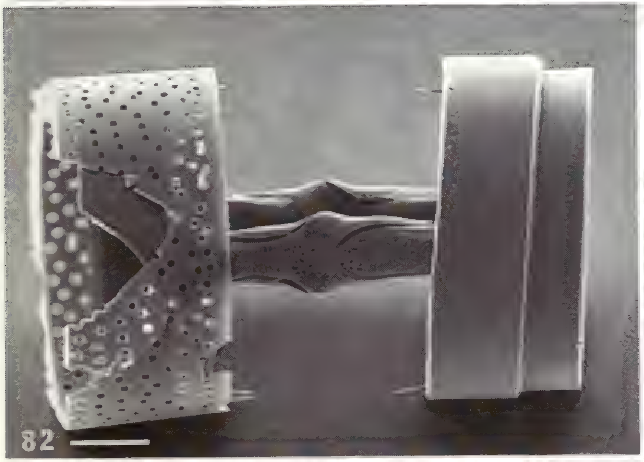
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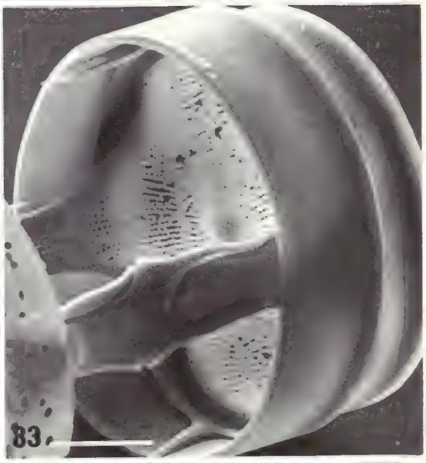
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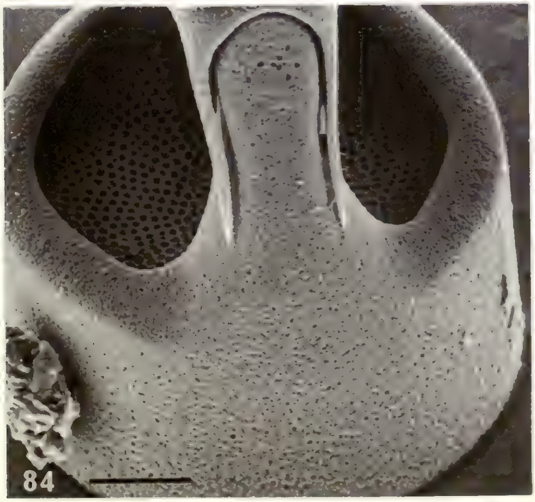
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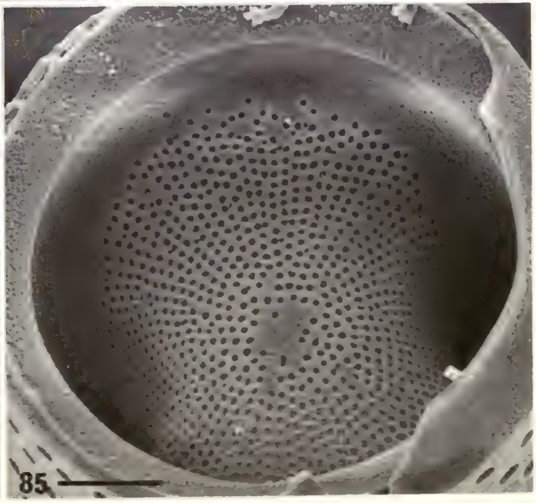
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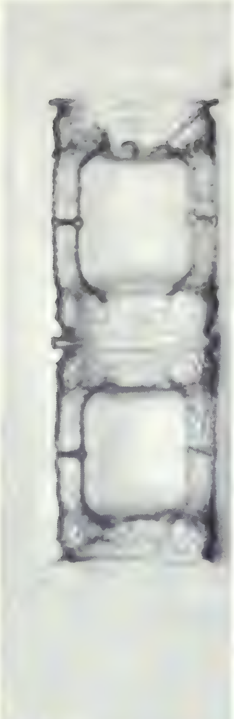
PLATE 12



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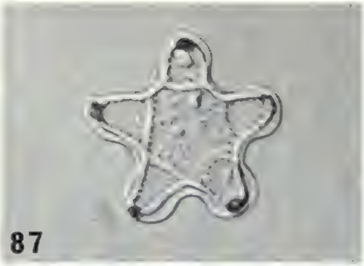

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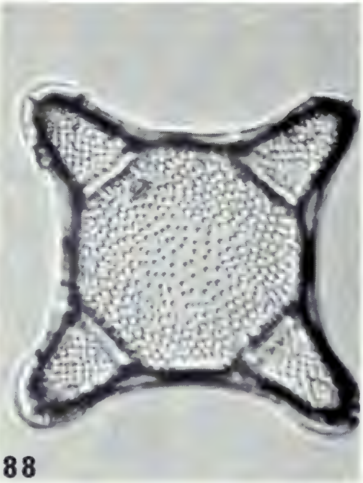

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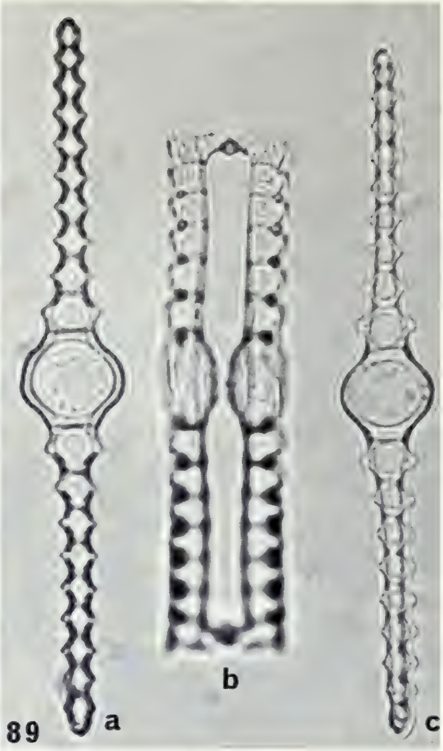

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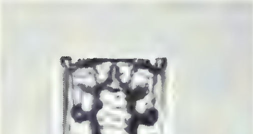

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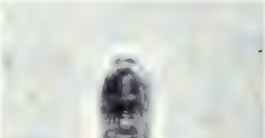

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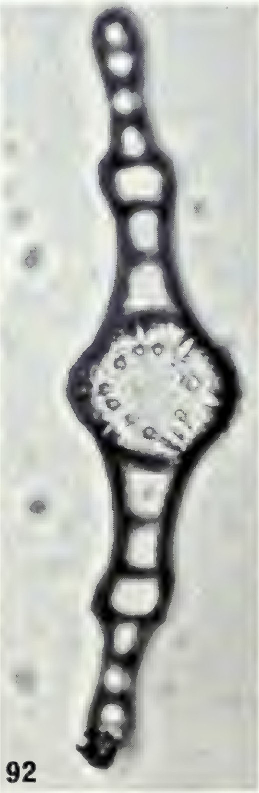

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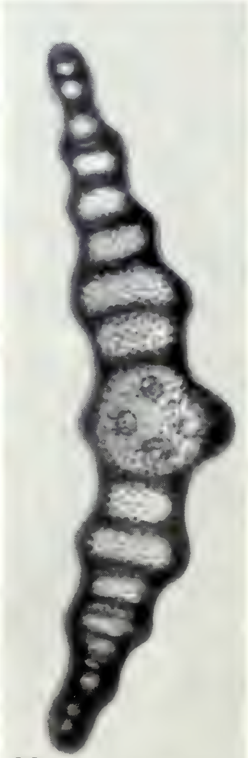

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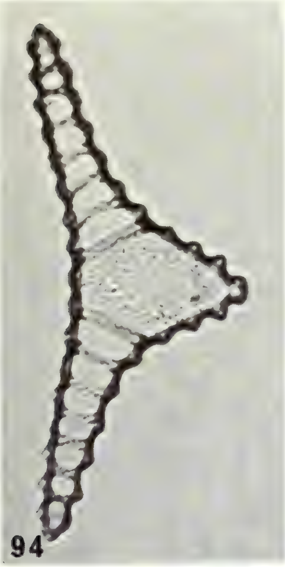
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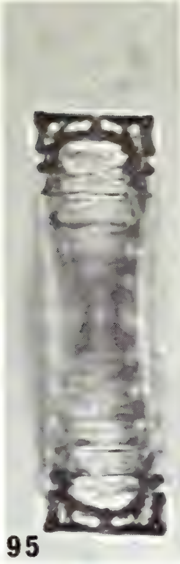
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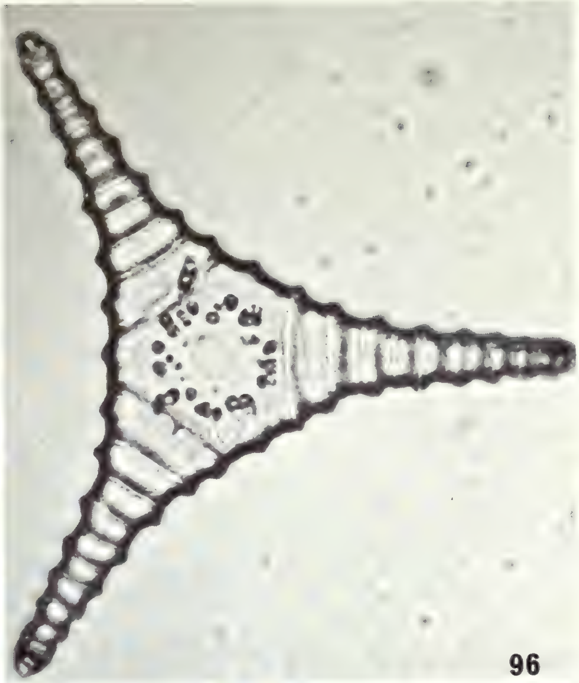
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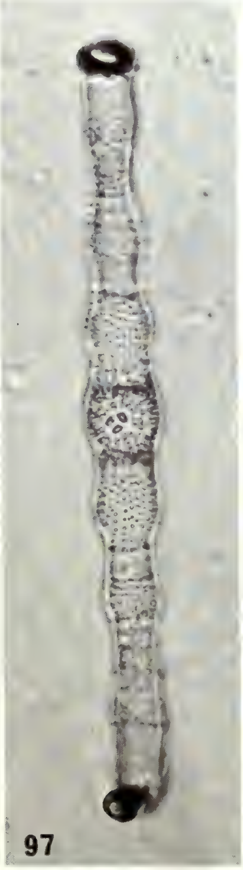
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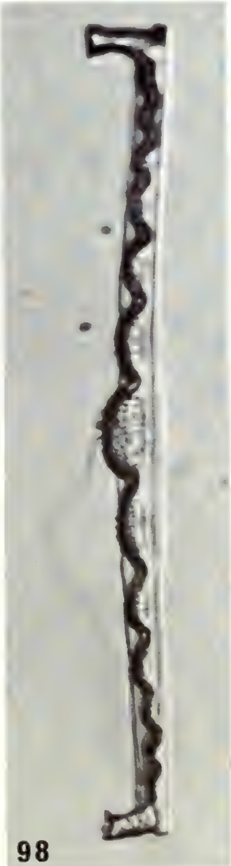
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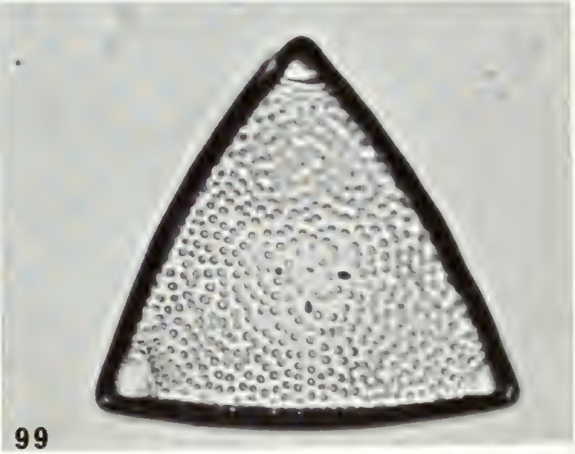
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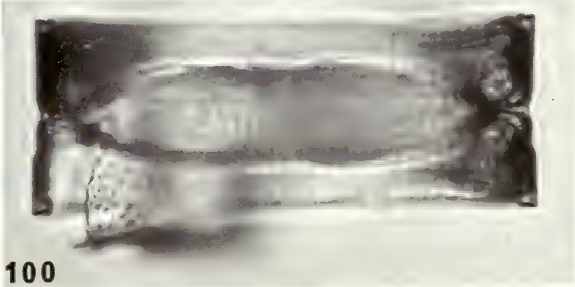
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